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Effects of Residual Tree Retention on Breeding Songbirds in Alberta's Boreal Mixed-Wood Forest

by

Rebecca Tittler ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

Department of Biological Sciences

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ABSTRACT

Residual tree retention has been proposed as a potential tool in the conservation of forest songbirds in logged landscapes. I censused songbirds in forested and logged sites in Alberta's boreal mixed-wood to investigate the effects of densities of residual trees varying from 10 to 133 trees/ha on songbird abundance and used artificial nests to investigate nest predation in the third year post-logging. I compared census data to data collected in the first year post-logging. Although forest songbirds were more abundant in forested than logged sites in both years, there were changes in species responses between years. There were few differences among forest species between sites with varying densities of residual trees. Nest predation did not differ among sites or stands adjacent to sites with varying densities of residual trees. In the third year post-logging, most forest songbirds were not affected by densities of residual trees varying within the range measured.

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CHAPTER 1

THESIS INTRODUCTION

Many populations of North American songbirds have declined significantly since the late 1960's or early 1970's (Wilcove and Whitcomb 1983, Robbins et al. 1989, Terborgh 1989, Robinson 1997, Sauer et al. 1997). Declines have been attributed to habitat loss and fragmentation on the breeding grounds in North America and on the tropical wintering grounds of neotropical migrants (Morse 1980, Terborgh 1989, Robbins et al. 1989, Askins et al. 1990). Rapid habitat loss and fragmentation are largely due to anthropogenic disturbance such as agriculture, forestry, and mining.

Songbirds are valued across North America for their diversity, aesthetic beauty, and as indicators of ecosystem response to disturbance. Bird watching is becoming an increasingly common past-time in North America as the human population ages and ecotourism grows (Foot 1996). Furthermore, since songbirds are relatively easy to census and are diverse in their habitat requirements, they may serve as good indicators of the effects of disturbance on natural communities as a whole (Adams and Barrett 1976, Steele et al. 1984, Croonquist and Brooks 1991).

Apart from habitat loss, perhaps the most deleterious effect of habitat fragmentation on breeding birds is the increase in nest predation and parasitism resulting from the creation of forest clearings such as agricultural fields and clearcuts (Gates and Gysel 1978, Robbins 1980, Ambuel and Temple 1983, Brittingham and Temple 1983, Andrén et al. 1985, Wilcove 1985, Andrén and Angelstam 1988, Johnson and Temple 1990, Vander Haegen and DeGraaf 1996). The junction of the forest ecosystem and that of the cleared land is called the forest edge. Forest edges often have higher rates of nest predation than the interior because high densities of nesting birds attract high densities of predators (Gates and Gysel 1978), edges serve as travel corridors (Bider 1968), and some clearings serve as predator or parasitoid sources (Brittingham and Temple 1983, Andrén 1995). Resulting high predation and parasitism levels are a major factor in the decline of songbird populations (Brittingham and Temple 1983, Wilcove 1985, Wilcove et al. 1986, Terborgh 1989, Askins et al. 1990).

The boreal mixed-wood forest of Alberta provides many songbirds with important

breeding habitat. The World Wildlife Fund classifies much of this area as outstanding in its ecological richness (Ricketts et al. 1998). The Western boreal forest is home to 95 species of songbirds (Smith 1993). However, the World Wildlife Fund also classifies much of the boreal mixed-wood as threatened or vulnerable habitat (Ricketts et al. 1998). At least 52 of its 95 songbird species declined across North America and 12 of the 95 declined in Alberta between 1966 and 1996 (Sauer et al. 1997).

The number of species declining in Alberta is likely to increase in the next few decades with increasing habitat loss and fragmentation. Until recently, Alberta's boreal mixed-wood forest was relatively unfragmented. However, recent developments in pulp and oriented strandboard technology have allowed for the profitable exploitation of the hardwood component of the mixed-wood, and this has resulted in approximately 195 662 km^2 of Alberta's forest being leased to companies for logging (D. Price, Alberta Environmental Protection, per. comm.). Although logging has already begun, far more land than has presently been logged is slated for logging in the next few decades. Companies are logging in a two- or three-pass system, whereby half or one-third of the area slated for logging is logged at each pass. In many areas, the second pass is scheduled to follow the first after a period of ten years. This system creates a patchwork of logged sites of different ages across the landscape which, coupled with the rapid expansion of gas and oil exploration and exploitation, will result in the loss of thousands of hectares of forest and in the creation of hundreds of thousands of kilometers of forest edge at the interface of recently-logged and forested or older logged stands. The loss of much of the old-growth mixed-wood may be permanent if logging rotation lengths are insufficient to allow regeneration to this point. Old-growth has been defined as "a stage of forest development characterized by more diversity of structure and function than that found in younger successional stages" (Thomas et al. 1988) and is attained at approximately 120 years in aspen-dominated mixed-wood stands (Stelfox 1995). At present the first pass is being logged, and has been completed in many areas.

Faced with growing concern over the detrimental effects of clearcutting, companies have begun to retain residual trees and snags in logged sites (Alberta Pacific Forest Industries Inc. 1996, Weyerhaeuser Canada Ltd. 1998). These trees and snags provide structural diversity to the regenerating stand (Rose and Muir 1995) and potential

habitat for wildlife such as woodpeckers (Dickson et al. 1981, Niemi and Hanowski 1984) and songbirds (Norton and Hannon 1997). However, industrial guidelines concerning the amount and structure of residual tree retention lack a strong scientific basis.

In 1994 and 1995, Norton and Hannon (1997) found that retention of approximately 20% to 50% of the trees provides more habitat for songbirds immediately following logging than retention of approximately 8%. Thus far, this is the only published study on the effects of residual tree retention on songbirds in the boreal mixed-wood forest of Alberta. Although it was a strong first step in investigating the conservation potential of residual tree retention, this study was limited in its scope: researchers examined only the year before and the year after logging and did not investigate anything other than turnover and songbird presence and abundance. In response to the need for more information on residual tree retention, I have continued and expanded on this study. In Chapter 2 of this thesis, I examine the influence of varying levels of residual tree retention on forest and open-area songbird abundances and investigate changes between the first and the third year post-logging. In Chapter 3, I examine the effects of residual tree retention on nest predation in and adjacent to logged sites with varying levels of residual tree retention, and compare these predation rates to rates recorded in forested control sites.

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CHAPTER 2

THE EFFECT OF RESIDUAL TREE RETENTION ON ABUNDANCES OF BREEDING SONGBIRDS IN ALBERTA'S BOREAL MIXED-WOOD FOREST

2.1 Introduction

Since the 1970's, there has been growing concern about declines in North American songbird populations (Wilcove and Whitcomb 1983, Robbins et al. 1989, Terborgh 1989, Robinson 1997). These declines have been attributed to forest fragmentation and habitat loss, both of which are largely due to anthropogenic disturbances such as urban development, agriculture, mining, and forestry (Morse 1980, Terborgh 1989, Robbins et al. 1989, Askins et al. 1990). The maintenance of much of North America's avifauna will depend on our ability to mitigate the effects of human development and resource exploitation on wildlife habitat (Terborgh 1989).

Alberta's boreal mixed-wood forest, like most forests of the world, is being rapidly fragmented by agriculture, logging, mining, and gas and oil activity. Although much of Alberta's forest is considered to be outstanding in its ecological richness and is classified as threatened or vulnerable habitat by the World Wildlife Fund (Ricketts et al. in press), 195 662 km^2 have been leased to companies for logging (D. Price, Alberta Environmental Protection, per. comm.). The boreal mixed-wood is being logged in a two- to three-pass clearcutting system, creating a patchwork mosaic of cutblocks across the landscape. We have very little idea what the long-term effects of such a disturbance will be on the landscape or on the wildlife in the area, nor do we know much about logging systems that might mitigate these potentially harmful effects.

As elsewhere, many researchers and some of the largest logging companies in Alberta have adopted the concept of ecosystem management, recognizing the diverse qualities and multiple uses of the land and managing with the general goal of *"protecting native ecosystem integrity over the long term"* through the use of *"scientific knowledge of ecosystem relationships"* (Grumbine 1994). In the context of logging, one of the strategies of ecosystem management is to mimic natural disturbance patterns (Alberta Pacific Forest Industries Inc. 1996, Rose and Muir 1997, Weyerhaeuser Canada Ltd. 1998). In a system that is naturally disturbed by fire, such as Alberta's boreal mixed-

wood forest, ecosystem management implies mimicking the variable intensity and frequency of wildfires. This may involve leaving pockets of live standing trees and snags in cutblocks after the harvest (Peterson and Peterson 1992). These trees and snags provide structural and age diversity to the regenerating stand and may facilitate conifer regeneration by providing shelter and seeds (Rose and Muir 1997).

Residual trees and snags may also provide habitat for forest songbirds. Thinning, strip-cutting, and leaving large clumps of residual trees (~0.54 ha) have been found to create highly diverse bird communities with fewer species losses than results from clearcutting in several forest types (Webb et al. 1977, Szaro and Balda 1979, Freedman et al. 1981, Merrill et al. 1998). Residual snags also provide foraging and nesting habitat for woodpeckers (Dickson et al. 1983, Niemi and Hanowski 1984). Logging companies in Alberta, as elsewhere, have incorporated recommendations as to leaving trees and snags in cutblocks into their operating guidelines (Alberta Pacific Forest Industries Inc. 1996, Weyerhaeuser Canada Ltd. 1998). However specific guidelines regarding the amount and structure of residual trees lack a strong scientific basis and we know little about vegetation characteristics that may be important in structuring bird communities in logged stands.

Norton and Hannon (1997) found that leaving residual trees (here referred to as "partial-cutting") benefits songbird communities in Alberta's boreal mixed-wood forest in the short term. Partial-cuts included 20-50% residual tree retention in the form of single and relatively small patches of trees and snags (0.001 to 1.147 ha, mean = 0.013 ha) in cutblocks ranging from 10.1 to 30.8 ha. Overall bird species richness and abundance were higher in partial-cuts than in clearcuts in the year immediately following a winter harvest, although both were lower in partial-cuts than in forested stands (Norton and Hannon 1997). Most of the species negatively affected by logging were shrub and tree nesters (Norton and Hannon 1997).

Like many other studies on the effects of logging (e.g., Szaro and Balda 1979, Scott and Gottfried 1993), Norton and Hannon's study included only the first breeding season following logging, while research indicates that the songbird community may change after the first few years. In a study on the effects of selective logging in the rainforest of Guiana, Thiollay (1992) found that the bird community changed

significantly in the first ten years following logging. Similarly, Welsh (1987) recorded changes in community structure in the first 33 years following selective logging in the boreal forest of Ontario. Temporal changes in community composition have also been documented in the sub-boreal forest of British Columbia following clearcutting (Pojar 1995) and in Alberta's boreal forest following wildfire (Schieck and Nietfeld 1995).

Abundances of forest birds may continue to decrease in the first few years following logging due to low reproductive success. Forest birds may crowd into remaining undisturbed areas or settle in sub-optimal habitat immediately following a disturbance (Hagan et al. 1996). However, since both of these strategies are likely to bring low breeding success, abundances in remaining undisturbed areas will return to pre-logging levels, while abundances in sub-optimal habitat may drop off entirely after a few years. This hypothesis is partially supported by research in the boreal mixed-wood: Schmiegelow et al. (1997) documented increased songbird abundances in remaining forested stands in the first year, followed by decreases in the second year after logging. If sites with high densities of residual trees (partial-cut sites) represent sub-optimal habitat, negative effects of logging on forest birds may not be evident until the second or third year after logging in these stands.

Since Norton and Hannon's (1997) study sites were logged in the winter, migratory species that might prefer to nest in logged than forested stands (open-area species) would likely not be recorded in logged stands in the year immediately following logging. Most migratory songbirds identify potential breeding habitat during the dispersal phase at the end of the breeding season and return to these identified sites the following season (Brewer and Harrison 1975, Morton 1992). Open-area species dispersing at the end of the first year before logging would not identify sites that were to be logged the following winter as potential breeding habitat. In fact, these species would not identify this potential habitat until the end of the first season following logging. Open-area species would therefore not be expected to move into logged sites until the second year post-logging.

With the above considerations in mind, I continued and expanded on Norton and Hannon's original study, repeating the bird census in the third year after logging. My objectives were: (1) to examine the effect of logging on songbirds, (2) to investigate the

effect of retaining high densities of residual trees by comparing songbird abundances in sites with varying densities of residual trees, and (3) to examine the role of other vegetation characteristics in determining songbird community structure in logged sites.

Although I have presented data on all species recorded in the appendices, I have focussed the discussion on species that were abundant the year before logging (1994), referring to them as common forest species throughout the text. I have identified species of concern as a sub-set of the common forest species, defining them as species recorded at significantly lower abundances in logged than forested sites after logging. I have also examined species common in logged sites, referring to these as open-area species. While rarer species are likely an integral part of the community and may disappear rapidly in response to habitat loss (Connor and McCoy 1979, Haila 1983), this study does not have a large enough sample size to encompass species that may breed at low densities or may be naturally rare in the area. By focusing on common species I hope to investigate the effects of logging and residual tree retention on the songbird community while avoiding drawing conclusions about rarer species based on occasional and perhaps incidental recordings.

My specific predictions concerning forest species and open-area species were that species of concern would be dependent on trees at some point in their life cycle (tree nesters and bark gleaners) and that open-area species would not be dependent on trees (ground nesters and foragers). I also predicted that forests species, and especially species of concern would decline and open-area species would increase in abundance in logged sites between the first and third year post-logging. Finally, I predicted that forest species, and especially species of concern recorded in logged sites would be associated with high densities of residual trees, while open-area species would be associated with low densities of residual trees.

2.2 Methods

2.2.1 *Study Area and Experimental Set-Up*

This study was carried out in an area of approximately 10 by 15 km in the boreal mixed-wood forest of Alberta (55°15'N, 113° 35"W). The boreal mixed-wood forest is dominated by a combination of hardwoods [trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifer*)] and softwoods [white spruce (*Picea glauca*), black spruce

(*P. mariana*), and jack pine (*Pinus banksiana*)] (Rowe 1972). Although the forest is naturally disturbed by fire, it is now the focus of extensive logging and gas and oil activity, resulting in a landscape fragmented by cutblocks, seismic lines, pipelines, roads, and clearings for well-heads.

Birds were censused in 12 sites in 1994 and 1995 and in 18 sites in 1997. In the winter of 1994-95, 9 of the 12 and 12 of the 18 sites were logged. Three of the 12 and 6 of the 18 sites were left forested and served as control sites. All sites were aspen-dominated mixed-wood stands greater than 130 years old before logging. Logging was done using feller-bunchers, skidders, and role-stroke delimbers (Norton and Hannon 1997). Logging operators were instructed to leave residual tree clumps and individual trees throughout the cutblocks, regardless of timber type, to establish six "partial-cuts", three with approximately 30% of the original trees retained ("low-residual partial-cuts") and three with 50% of the original trees retained ("high-residual partial-cuts"). All sites were between 10 and 35 ha in size and sizes were stratified across four treatments (clearcuts, low-residual partial-cuts, high-residual partial-cuts, and forested controls). However, final cutblocks varied in residual tree retention far more than intended, so these treatment types were ignored for the purpose of this study, as described in the section 2.2.4 below. All sites were a minimum of 300 m apart and forested controls were at least 400 m from any logged stands. To control for possible adjacency effects, all sites were located adjacent to old, aspen-dominated mixed-wood, not to bog, wetland, or conifer-dominated stands.

2.2.2 *Bird Censuses*

Census stations were set up 200 m apart in each study site and birds were censused using a 5 minute, 100 m fixed radius point-count technique, as described by Ralph et al. (1993). I established two to six census stations per site, depending on the size of the site. In logged sites, all stations were a minimum of 50 m from the edge of the cutblock. Each site was censused between dawn and 10:00 AM at approximate 10-day intervals three times from the first week of June to the first week of July 1994, and four times from the last week of May to the first week of July 1995 and 1997. To minimize observer and time-of-day biases, I rotated observers so that each site was censused by at least two different observers and I arranged the order of census so that all sites were

censused at dawn at least once each season. Singing males were assigned an abundance score of 1 while calling and silent birds were assigned an abundance score of 0.5. Censuses were not performed under windy (>3 on the Beaufort scale) or rainy conditions. This censusing protocol was identical to the protocol used by Norton and Hannon (1997).

Norton and Hannon (1997) calculated species abundances per station as the maximum sum of abundance scores recorded at each census station in any one of the three or four censuses performed throughout the season. Since census stations were only 200 m apart and the census radius at each station was 100 m, there was a high probability of counting one individual as two or more individuals by recording them at different stations on different visits using Norton and Hannon's technique. To minimize this risk of "double-counting" individuals, I calculated abundances per species as the maximum number of observations per site (all stations combined) in any one of the three or four censusing rounds and divided this total by the number of stations to give a mean abundance per station. Observers were instructed to avoid recording one individual at more than one station and adjacent stations were censused one after the other in all years. I re-analyzed the 1994 and 1995 data accordingly. I did not calculate a density per hectare because I did not want to imply that I had obtained actual nesting densities: a more intensive territory-mapping program would be necessary to address this issue. To reduce any confounding effects of observer error, I excluded any species recorded only once in either the forested or logged sites. I also excluded all observations of birds flying over the sites based on the assumption that this does not represent true habitat use. Finally, I excluded woodpeckers (*Picoides* species) and all Black-capped Chickadees (*Poecile atricapillus*) because they breed early in the season and are not best censused using a 100 m fixed-radius point-count technique at the time of year at which these censuses were performed.

2.2.3 *Vegetation*

Vegetation was sampled in July and August of 1994 and 1997. Three 0.04 ha vegetation plots were sampled for each point count station 30 m from the station at 0°, 120°, and 240° respectively. I measured canopy cover with a spherical densiometer and canopy, subcanopy, and tall shrub height (height of the tallest shrub in the plot) with a clinometer. I recorded species and classified diameter at breast height (DBH) of all trees

(class 1: 8-15 cm; class 2: 15-23 cm; class 3: 23-38 cm; and class 4: >38 cm), and species, height, percent bark cover, and DBH of all snags in the plot. I calculated mean DBH and basal area (BA) of trees based on the median of each DBH class. I estimated percent ground cover of coarse woody debris, shrub, forb, grass, moss and fern, and leaf litter visually in four 1 m^2 plots located at 3 m in each of the four cardinal directions from the centre of each 0.04 ha main plot. I counted shrub stems by species in five similar 1 m^2 plots at the centre and at 5 m from the centre of each main plot and measured leaf litter depth 3 m from the centre of the plot in four cardinal directions. I also recorded species and DBH classes of all saplings and poles within a 5 m radius plot centred on the main plot (class 1 = <2.5 cm; class 2 = 2.5 cm to 8 cm).

Norton and Hannon (1997) used aerial photographs of logged sites after logging and densiometer readings from the same sites before logging to calculate the percentage of trees left standing in each site. They classified the treatment into four categories based on percent retention: clearcuts (~8%), partial-cuts with low retention of residual trees (~30% retention), partial-cuts with high retention of residual trees (~40%), and forested controls (Norton and Hannon 1997). To standardize the pre-harvest and post-harvest measurements, limit the classification of treatment to the 100 m radii sampled, and simplify interpretation of results for operators and researchers working on the ground, I re-calculated the residual tree retention based on vegetation data collected on the ground. I calculated extent of disturbance by adding up the total number of trees and snags greater than 15 cm DBH in each of the three associated plots and dividing this total by 0.12 ha (0.04 ha * 3) to give a density of trees and snags per ha. This measure is referred to as residual tree density throughout the text (see Appendix 2.1 for values).

2.2.4 *Analyses*

While Norton and Hannon (1997) used analyses of variance (ANOVA's) to examine the effects of their four treatments on songbird richness, abundance, and turnover, I used regressions to examine the effects of residual tree density on songbird abundances in logged stands. I based this decision on the findings that, when disturbance was taken as tree density rather than as percent cover based on aerial photos, (a) some of Norton and Hannon's sites were inconsistent with the treatment categories (i.e., one site with a relatively high density of residual trees was classified by Norton and Hannon as a

clearcut), and (b) density of residual trees represented a continuum rather than distinct treatment categories. Results reported from 1994 and 1995 differ slightly from those reported by Norton and Hannon (1997) due to these differences in analysis.

In all analyses of bird census data, I used an α-level of 0.10 to reduce the probability of committing a Type II error (Schmiegelow et al. 1997). Bonferroni adjustments were used whenever multiple comparisons were performed (Zar 1984). I tested the power of each analysis using the program G-Power (Faul and Ehrdfelder 1992). If power was moderate to high (≥ 0.65, $\alpha = 0.10$) (Cohen 1988), I performed conventional statistical tests, selecting between parametric and non-parametric tests based on homogeneity of variance (examined using a Levene test) and normality (examined using a Kolmogorov-Smirnov goodness of fit test) (Zar 1984). Unless otherwise specified, I used SPSS (version 6.0 or 6.1) for all analyses.

If power was low (< 0.65, $\alpha = 0.10$) (Cohen 1988), I analyzed data using randomization tests. I replaced paired and independent sample t-tests with randomized t-test using the program RANDCOMP (Brzustowski 1997). This program calculates the observed mean differences between two groups then randomly selects samples from each group 1000 times and compares the observed mean differences with the distribution of randomly selected mean differences. RANDCOMP provides a p-value that indicates whether or not the observed distribution is significantly different from the randomly selected distribution but it does not provide a test-statistic. I replaced linear regressions with randomized linear regressions using the program RT (Manly 1996). This program functions similarly to RANDCOMP, first performing a linear regression on the dataset, then randomly rearranging the observations of the dependent variable in 1000 different ways and performing linear regressions on each of these 1000 randomized data sets. RT provides an F-statistic for the observed regression and for each of the randomized regressions, and I extrapolated p-values based on the number of randomized F-statistics larger than the observed F-statistic.

I used Phi-Square indices of dissimilarity and Jaccard indices of similarity to investigate community turnover in individual sites between years. The Jaccard Index uses presence-absence data to calculate an index of similarity ranging from 0 to 1, with 1 being the most similar (all species in common between sites) and 0 being the least similar

(no species in common between sites) (Krebs 1989). To examine turnover based on abundance data, I used a Phi-Square Index of dissimilarity. The Phi-Square Index also ranges from 0 to 1, with 0 being the most similar and 1 the least similar (Krebs 1989). To simplify interpretation, I adjusted all Jaccard indices by subtracting them from 1 so that 0 was the most similar (lowest turnover) and 1 the least similar (highest turnover) for both indices.

To investigate the influence of nesting guilds, foraging guilds, and migratory strategy on species responses, I performed contingency analyses using a log-likelihood ratio on the number of species of each guild or strategy increasing and decreasing in abundance with logging and extent of logging. The log-likelihood, when doubled, approximates the Chi-square distribution and is used when observed and expected values are too small to use a Chi-square or G-test (Zar 1984). Species were grouped by nesting and foraging guilds according to Ehrlich et al. (1988), and by migratory strategy according to Godfrey (1986).

2.2.4.1 *Species and Community Response to Logging*

I examined differences between logged and forested sites in 1995 and 1997 by comparing overall and individual species abundances using t-tests for independent samples, Mann-Whitney U tests, or randomized t-tests, depending on power, normality, and homogeneity of variance, as described above (Zar 1984, Cohen 1988). I examined two sets of species: common forest species and open-area species. Common forest species were defined as those for which at least 10 individuals had been recorded in all 12 censused sites combined (at least 2% of the birds recorded) before logging (in 1994), as suggested by Schieck and Nietfeld (1995). The 17 species identified as common forest species were the American Redstart, Black-throated Green Warbler, Brown Creeper, Canada Warbler, Chipping Sparrow, Least Flycatcher, Mourning Warbler, Ovenbird, Rose-breasted Grosbeak, Red-eyed Vireo, Swainson's Thrush, Warbling Vireo, Western Tanager, Winter Wren, White-throated Sparrow, Yellow Warbler, and Yellow-rumped Warbler (refer to Appendix 2.2 for scientific names). Species of concern were identified from among these common forest species as those with abundances significantly lower in logged than forested sites in 1997. Open-area species were defined as those with significantly higher abundances in logged than forested sites in 1997.

I also compared turnover in common forest and open-area communities in logged and forested sites between pre- and post-logging years. I used Jaccard and Phi-Square indices to examine turnover between 1994 and 1995, between 1994 and 1997, and between 1995 and 1997 for both communities. As above, I analyzed these data using t-tests, Mann Whitney U tests, or randomized t-tests, depending on normality, homogeneity of variance, and power.

2.2.4.2 *Effect of Residual Trees*

Depending on the power of the tests, I used linear regression or randomized linear regression models to investigate the effect of tree density on individual species abundances and on total abundance of common forest and open-area species in logged sites in 1995 and 1997. Similarly, I used linear regressions or randomized linear regressions on Phi-Square and Jaccard indices to investigate the effect of varying levels of residual tree density on turnover of common forest and open-area communities in logged sites between 1994 and 1997. For analyses of community turnover, I used the number of trees recorded in each site in 1997 as a percentage of those recorded in the same sites in 1994, as opposed to using the simple calculated tree densities as a measure of disturbance (see Appendix 2.1 for values).

2.2.4.3 *Changes Between the First and Third Year Post-Logging*

I examined changes in logged and forested sites between 1995 and 1997 using paired t-tests, Wilcoxon paired-sample, or randomized t-tests, depending on normality, homogeneity of variance, and power, as described above. Specifically, I investigated changes in overall abundance and individual species abundances of common forest and open-area birds. For these comparisons, I restricted 1997 datasets to the 12 sites censused in 1995. I also examined differences in Jaccard and Phi-Square indices to investigate whether turnover of common forest and open-area communities in logged sites was different between the 1994-1995 and 1994-1997 comparisons. I restricted all datasets to three rounds of point counts and 12 sites for comparisons involving the 1994 data.

2.2.4.4 *Vegetation Characteristics and Songbird Community*

I used direct ordination analysis and the program CANOCO (version 3.10) to investigate environmental characteristics associated with songbird community

composition in logged sites. These analyses are designed to investigate relationships between environmental variables and community composition by arranging species along composite axes which represent combinations of measured environmental variables (terBraak 1995).

I performed a detrended correspondence analysis (DCA) to determine whether measured songbird response to environmental variables was linear or unimodal. DCA provides a measure of the length of the environmental gradient for each axis. Based on an environmental gradient of 1.59 on my first DCA axis, I used redundancy analysis (RDA) for linear response data to investigate the effect of environmental variables on songbird communities, as suggested by terBraak (1995).

I selected a model using the forward-selection option in CANOCO ($p < 0.25$). This option allows for the inclusion of explanatory variables in a step-wise fashion, adding the variable that explains the largest portion of the remaining unexplained variance in the species data at each step (terBraak 1990). Explanatory variables tested included number of stations per site and mean values (per site) of all measured vegetation variables. The number of stations per site was included as a measure of the size of each site, as more species might be recorded in larger sites. As recommended by terBraak (1995), I transformed all environmental variables (mean = 0, standard deviation = 1) before using them in the RDA to allow for comparison between environmental variables with long and short measured gradients. I performed Pearson's bivariate correlations to ascertain that none of the variables included in the model were highly correlated (i.e., correlation coefficients ≥ 0.75).

2.3 Results

2.3.1 *Forest Species*

In 1995, total abundance of common forest birds was significantly higher in forested than in logged sites (Table 2.1). Abundances of 11 individual species were also significantly higher in forested than logged sites (Figure 2.1). These were the Yellow-rumped Warbler, Red-eyed Vireo, American Redstart, Black-throated Green Warbler, Rose-breasted Grosbeak, Swainson's Thrush, Yellow Warbler, Ovenbird, Brown Creeper, Canada Warbler, and Mourning Warbler.

Total abundance of common forest birds was also significantly higher in forested

than in logged sites in 1997 (Table 2.1) and abundances of 10 individual common forest species were significantly higher in forested than in logged sites, but this group of negatively affected species was slightly different than in 1995 (Figure 2.2). The Rose-breasted Grosbeak, Yellow Warbler, and Mourning Warbler were not recorded at lower abundances in logged than forested control sites in 1997 (Figure 2.2), although they were in 1995 (Figure 2.1). The Winter Wren, Warbling Vireo, and Western Tanager were not recorded at lower abundances in logged sites in 1995 (Figure 2.1), but were in 1997, the latter two species disappearing from logged sites (Figure 2.2). I defined species recorded at significantly lower abundances in logged than in forested sites in 1997 as species of concern. These were: the American Redstart, Black-throated Green Warbler, Brown Creeper, Canada Warbler, Ovenbird, Red-eyed Vireo, Swainson's Thrush, Warbling Vireo, Western Tanager, and Winter Wren (Figure 2.2).

Differences in species abundances were reflected in indices of community turnover among common forest songbirds. In terms of species presence (Jaccard), turnover between years was greater in logged than forested sites for all three annual comparisons (1994-1995, 1994-1997, and 1995-1997) (Table 2.2). In terms of species abundance (Phi-Square), turnover between 1994 and 1995 and between 1995 and 1997 was significantly higher in logged than forested sites (Table 2.2).

There was no effect of residual tree density on overall abundance of common forest species in 1995 or in 1997 (Table 2.3). Similarly, turnover in common forest bird communities was not affected by residual tree density in the 1994-95 or the 1994-97 comparison (Table 2.4). In 1995, the American Redstart, Mourning Warbler, Swainson's Thrush, and Yellow Warbler increased in abundance with increasing residual tree density but by 1997 the only species increasing significantly with tree density was the Yellow-rumped Warbler (Table 2.3). No common forest species decreased with increasing tree density in either year.

Total abundance of common forest birds did not change significantly in logged or forested sites between 1995 and 1997 (Table 2.1). Similarly, turnover in the community of common forest birds from 1994 to 1995 was no different than between 1994 and 1997 (Table 2.5). However, abundances of seven common forest species changed in logged sites between 1995 and 1997 (Figure 2.3). The Brown Creeper, Warbling Vireo, and

Western Tanager all disappeared from logged sites while the Chipping Sparrow decreased significantly in logged sites between years (Figure 2.3). The Ovenbird appeared in logged sites in 1997 and the Rose-breasted Grosbeak and Mourning Warbler increased significantly in abundance between years (Figure 2.3). None of these species changed in abundance in forested sites between years (Figure 2.4). No species increased significantly in abundance in forested sites between 1995 and 1997 and the only species to decrease was the Yellow-rumped Warbler (Figure 2.4).

2.3.2 *Open-Area Species*

Although no species were recorded at significantly higher abundances in logged than forested sites in 1995 (Figure 2.1), eight species were recorded at higher abundances in logged than in forested sites in 1997 (Figure 2.2). These were classified as open-area species. These species were the Alder Flycatcher, Clay-coloured Sparrow, Common Yellowthroat, LeConte's Sparrow, Lincoln's Sparrow, Song Sparrow, White-throated Sparrow, and Mourning Warbler. The latter two were also classified as common forest species but apparently preferred the logged sites in 1997. The Alder Flycatcher, Clay-coloured Sparrow, Lincoln's Sparrow, Mourning Warbler, and White-throated Sparrow were recorded in logged sites in 1995, but, except for the last two species, abundances were low (Figure 2.1). The Mourning Warbler was recorded at significantly lower abundance in logged than forested sites in 1995 (Figure 2.1).

Species level differences between logged and forested sites were reflected in the analyses of community indices. In terms of species presence (Jaccard), turnover between 1994 and 1995 and between 1994 and 1997 was significantly higher in logged than in forested sites (Table 2.2). In terms of species abundance (Phi-Square), turnover between 1994 and 1997 was also significantly higher in logged than in forested sites. I did not analyze the 1994-1995 comparison because there was no turnover of open-area species in logged or forested sites.

Total abundance of open-area birds was not affected by varying densities of residual trees in logged sites in 1995 but abundance increased with decreasing residual tree density in 1997 (Table 2.3). Similarly, no species increased significantly in abundance with decreasing residual tree density in logged sites in 1995 but the Lincoln's Sparrow responded in this way in 1997 (Table 2.3). No open-area species increased with

increasing residual tree density in either year (Table 2.3).

The Common Yellowthroat, LeConte's Sparrow, Lincoln's Sparrow, and Mourning Warbler increased significantly in abundance in logged sites between 1995 and 1997 (Figure 2.3). Turnover of the open-area community was significantly higher in the 1994-97 comparison than in the 1994-95 comparison in terms of species abundance (Phi-Square), although not in terms of species presence (Jaccard) (Table 2.5). Only the Mourning Warbler and the White-throated Sparrow were recorded in forested sites in both 1995 and 1997 and neither changed significantly in abundance between years (Figure 2.4). The LeConte's Sparrow was recorded at low abundances in forested sites in 1997 and the Lincoln's Sparrow in 1995 but neither of these changed significantly in abundance between years (Figure 2.4).

2.3.3 *Role of Nesting Guild, Foraging Guild, and Migratory Strategy*

Species of concern were not predicted by nesting guild, foraging guild, or migratory strategy in either 1995 or 1997 (Tables 2.6, 2.7, and 2.8). This group of species included species of all identified nesting and foraging guilds and of all migratory strategies in 1997 and species of all but the cavity nesting guild in 1995. However, only 1 (6%) of the 17 common forest species was a cavity nester.

Neither foraging guild nor nesting guild nor migratory strategy was a good predictor of species that increased with increasing residual tree density in logged sites in 1995 (Tables 2.6, 2.7, and 2.8). No species decreased with increasing residual tree density in 1995. These analyses were not repeated on the 1997 data because only one species increased with increasing tree density, while only one species decreased. The Yellow-rumped Warbler, the one species increasing, is a foliage gleaner, shrub nester, and a short-distance migrant, and the Lincoln's Sparrow, the one species decreasing, is a ground nester and forager and a neotropical migrant. However, numbers were too low to draw conclusions about the effect of foraging or nesting guild.

Neither nesting guild nor foraging guild nor migratory strategy was a good predictor of open-area species: among the open-area birds were species from the two most common nesting guilds, the three most common foraging guilds, and the two most common migratory strategy groups (Tables 2.6, 2.7, and 2.8). The one nesting guild not represented among the open-area species was the cavity nesting guild, but only 8% (3 of

36) of all birds recorded in 1997 were cavity nesters. The one foraging guild not represented was the bark foraging guild, but only 8% (3 of 36) of all birds recorded in 1997 were bark foragers. The one migratory strategy not represented was the resident group, but only 6% (2 of 36) of all birds recorded in 1997 were residents. These analyses were not performed on the 1995 data because no species were recorded at higher abundances in logged than forested sites in this first year after logging.

2.3.4 *Vegetation Characteristics and Songbird Community*

Of the 17 common forest species, I excluded all but the Yellow-rumped Warbler, Least Flycatcher, White-throated Sparrow, Chipping Sparrow, Yellow Warbler, Mourning Warbler, Rose-breasted Grosbeak, and Red-eyed Vireo from the RDA due to total abundances lower than 5 (0.7% of all birds recorded) in logged sites in 1997. The only species of concern included was the Red-eyed Vireo. Since all open-area species were abundant in logged sites in 1997, I did not exclude any of these species.

The model that explained the most variance in common forest and open-area species in logged sites included conifer basal area (BA), number of deciduous trees between 8 and 15 cm DBH (small deciduous trees), and percent grass cover as explanatory variables. Deciduous trees of 8 to 15 cm DBH were too large to be the result of three years of regeneration in these stands and these therefore represent a class of residual trees left after logging. Of the three variables included in the RDA, number of small deciduous trees was most strongly correlated with the first axis and both number of small deciduous trees and conifer BA had a significant effect on this axis (Table 2.9). Both of these variables were also correlated with the second axis and conifer basal area had a significant effect on this axis (Table 2.9). Since the first two axes accounted for 79.5% of the species-environment relation (52% on the first axis), I considered only these two axes in interpreting the data. With eigenvalues of 0.240 and 0.127 respectively, the first two axes explained a total of 36.7% of the variance in species data (24% on the first axis).

Common forest species were largely associated with percentages of grass cover lower than the mean and numbers of small deciduous trees higher than the mean in logged sites, with the Least Flycatcher and Yellow-rumped Warbler being the most extreme examples of this pattern (Figure 2.5). The Yellow-rumped Warbler and the

White-throated Sparrow were associated with conifer basal area higher than the mean but the other common forest species did not show the same pattern (Figure 2.5).

The open-area species were associated with grass cover higher than the mean and number of small deciduous trees lower than the mean, except for the Mourning Warbler, White-throated Sparrow, and Clay-coloured Sparrow (Figure 2.5). The Clay-coloured Sparrow was associated with the mean of both variables and the Mourning Warbler and White-throated Sparrow were both associated with number of small deciduous trees slightly higher and grass cover slightly lower than the mean (Figure 2.5). All but the White-throated Sparrow were associated with conifer basal area lower than the mean (Figure 2.5).

None of the three variables included in the RDA were highly correlated with residual tree density. Small deciduous trees had the highest correlation with residual tree density, with a correlation coefficient (R^2) of 0.638, while grass had a correlation of -0.456, and conifer basal area, of 0.053. The lack of a strong correlation is reflected in the fact that study sites did not cluster out on the RDA according to residual tree density (Figure 2.6). Although the sites associated with conifer basal area and number of small deciduous trees higher than the mean had high residual tree density (#8 and #12 associated with conifer BA and #10 and #12 associated with small deciduous trees), the site with the second highest residual tree density (#11) was not associated with either number of small deciduous trees or conifer basal area higher than the mean. Furthermore, although the two sites most highly associated with grass cover higher than the mean were the two sites with the lowest residual tree density (#1 and #2), the third lowest site (#3) was not particularly associated with grass cover higher than the mean. Site #7 was associated with grass cover higher than the mean and small deciduous trees and conifer basal area lower than the mean but was intermediate in terms of residual tree density, indicating that residual trees were mostly deciduous trees of large rather than small diameter. These trees may have been highly clumped, providing space for high levels of grass cover between clumps of residual trees.

Comparison of the species (Figure 2.5) and site (Figure 2.6) biplots indicates that open-area species were common in the two sites with the lowest density of residual trees (#1 and #2) and in one of the sites with intermediate densities of residual trees (#7).

Least Flycatchers were positively associated with a site with high densities of residual trees (#10). Yellow-Rumped Warblers were positively associate with two sites with high (#10 and #12) and one with intermediate densities of residual trees (#8). The remaining species indicated little association with specific study sites. These species-site relationships may be explained by the species-vegetation and site-vegetation relationships discussed above.

2.4 Discussion

2.4.1 *Species and Community Response to Logging*

As predicted, there were significant changes in songbird abundances between the first and third year post-logging. All forest species decreasing in abundance in logged sites between the two years are shrub or tree nesters and all but one are bark or foliage gleaners. The Warbling Vireo and Western Tanager are both foliage gleaners, the Brown Creeper is a bark forager, and the Chipping Sparrow is a ground forager (Ehrlich et al. 1988). Contrary to predictions, the Rose-breasted increased in abundance in logged sites between 1995 and 1997, although it nests in shrubs or trees (Ehrlich et al. 1988). The other two species increasing in abundance were the Ovenbird and Mourning Warbler, the former a ground nester and forager and the latter a ground nester and foliage gleaner (Ehrlich et al. 1988). The American Redstart, Mourning Warbler, Swainson's Thrush, and Yellow Warbler were all associated with high densities of residual trees in 1995 but none disappeared from these sites between 1995 and 1997. Significant changes in species abundances between the first and third year post-logging were reflected in the higher turnover between 1994 and 1997 than between 1994 and 1995. The reduction and loss of species between years may be due to their initial failure to breed successfully in logged sites (as per Hagan et al. 1996) and to competition with species better adapted to the early successional stage of the logged sites (Ambuel and Temple 1983). Increases in abundances of Mourning Warblers (initially recorded at lower abundances in logged than forested sites) may be due to the rapid regeneration of the aspen stands in which the study took place; in many stands, aspen was 1 to 1.5m in height by 1997 (personal observation).

I identified ten species of concern based on the 1997 data. These species were the American Redstart, Black-throated Green Warbler, Brown Creeper, Canada Warbler,

Ovenbird, Red-eyed Vireo, Swainson's Thrush, Warbling Vireo, Western Tanager, and Winter Wren. Although overall abundance of common forest birds did not change significantly between 1995 and 1997, there were changes in species abundances and in species composition in logged sites between years and I would have identified different species of concern had I examined only the 1995 data. Species found at lower abundances in logged than forested sites three years after logging are more likely indicative of long-term negative effects than those responding in this way in the initial post-logging year.

All species of concern except the Red-eyed Vireo and the Ovenbird have been classified by Schieck and Nietfeld (1995) as moderately or strongly associated with old forest in the boreal mixed-wood. Both the Red-eyed Vireo and the Ovenbird are associated more strongly with mature (50-65 year old) than with either old (120 year old or older) or young (20-30 year old) mixed-wood (Schieck and Nietfeld 1995).

The Yellow-rumped Warbler was recorded at lower abundances in logged than forested sites in the year immediately following logging (1995), and decreased in forested sites between 1995 and 1997. I was initially concerned that it might be decreasing across the landscape, however, the latter concern is not supported by other data from the area (F.K.A. Schmiegelow and S.J. Hannon unpublished data, S. Song unpublished data). Recorded changes in abundance in this study may be the result of natural variation in the population or of variation in the timing of nesting. As short-distance migrants (Godfrey 1986), Yellow-rumped Warblers are the first of the migratory songbirds to arrive in the area and also the first to begin singing (R. Tittler unpublished data). Since I began censusing only once the majority of birds had arrived in the study area, I may have underestimated the abundance of Yellow-rumped Warblers in both years. If Yellow-rumped Warblers arrived earlier in 1997 than in 1995, I may have missed more of them in the third than in the first year after logging. Censuses for another study in the area began 10 days earlier than in this study in both 1995 and 1997 and no change between years was recorded (F.K.A. Schmiegelow and S.J. Hannon unpublished data).

Whereas many forest species were recorded at lower abundances in logged than forested sites immediately following logging, they were not replaced by open-area birds in logged sites until after this first year. Open-area species were defined as those

recorded at significantly higher abundances in logged than forested sites. In 1995, no species demonstrated this positive response to logging but in 1997 eight species fit this description. The Common Yellowthroat, LeConte's Sparrow, and Song Sparrow were not recorded in any sites before 1997. The Alder Flycatcher and the Clay-coloured Sparrow were recorded in logged sites in 1995, but abundances were very low. The Lincoln's Sparrow and Mourning Warbler were not more abundant in logged than forested sites until 1997; in fact, the Mourning Warbler was less abundant in logged than forested sites in 1995. All open-area species have been defined as generalists or species preferring young stands, except the Mourning Warbler and the White-throated Sparrow (Schieck and Nietfeld 1995). The Mourning Warbler and White-throated Sparrow have been defined by Schieck and Nietfeld (1995) as preferring old stands, however, the youngest stands censused in their study was 20 years old, far older than my 3-year-old logged sites. These two species may be out-competed in the second and third decade after logging by species better adapted to this successional stage, such as the Hermit Thrush or the Connecticut Warbler (Schieck and Nietfeld 1995).

Open-area species may not have increased in abundance or appeared in logged sites in the year immediately following logging because (a) the newly logged sites were not yet suitable habitat, or (b) open-area birds lacked knowledge of these newly disturbed areas. The logging was done in the winter of 1994-95. Since birds disperse at the end of the breeding season to seek possible nesting areas for the following season (Brewer and Harrison 1975, Morton 1992), dispersing open-area birds would not have perceived these areas as potentially suitable habitat in 1994. These same species dispersing at the end of the 1995 season would have discovered these newly disturbed sites and may have returned to breed in 1996. By 1997, yet another cohort of birds would have had the chance to discover the area.

The loss of species from logged sites was likely due to the lack of suitable habitat. The Canada Warbler was not recorded in logged sites in either of the post-logging years. The Brown Creeper, Western Tanager, and Warbling Vireo were recorded in logged sites immediately following logging but not three years later, indicating that they may initially have settled in sub-optimal habitat and left following poor breeding success (Hagan et al. 1996).

Some species of concern persisted in logged sites in both years following logging. These included the American Redstart, Black-throated Green Warbler, Ovenbird, Red-Eyed Vireo, Swainson's Thrush, and Winter Wren. The presence of a few individuals may indicate that some suitable habitat was available. However, the limitations of the point count technique must be considered in interpreting these results. Although the point count technique assumes that singing birds represent breeding pairs (Ralph et al. 1993), individuals may not be breeding where they are singing (Ambuel and Temple 1983). Selecting singing posts in logged sites may allow for greater song transmittance (Kroodsma 1984) but birds may be breeding in adjacent forested stands. In this study, all logged stands were adjacent to old forested stands, which would provide adequate nesting opportunities for old-growth species. Forest birds recorded singing in logged sites may also have been unmated males, as recorded for Ovenbirds in other sub-optimal habitats (i.e., small forest tracts) in Missouri (Gibbs and Faaborg 1990, Van Horn et al. 1995). Merrill et al. (1998) did record Ovenbirds nesting in residual tree patches, but these patches were much larger than those considered in this study (mean = 0.540 ha as opposed to 0.013 ha in this study). Researchers in the boreal mixed-wood have noted Ovenbirds nesting in stands adjacent to logged sites and flying out into logged sites to sing from residual trees (Lambert 1998).

A rigorous nest monitoring program would be necessary to investigate whether species recorded in logged sites were nesting in these stands. Although I initially planned to attempt such a project, logistic constraints prevented me from doing so. It would also be useful to return to the sites once the old stands adjacent to the logged stands had been logged. Since the study area is designated for this second pass in the year 2004, just ten years after the initial logging, I predict the disappearance of any species using logged sites for singing but relying on adjacent old stands for nesting at this time.

2.4.2 *Effect of Residual Trees*

Response to high densities of residual trees also changed between the first and the third year post-logging. There was a positive effect of high densities of residual trees on abundances of common forest species and five individual species in the first year post-logging but a positive effect on only one species in the third year, with no effect on total abundance of common forest birds. There was no relationship between total abundance

of open-area birds and density of residual trees in the first year post-logging but there was a significant negative relationship in the third-year post-logging. At a species level, abundance of the Lincoln's Sparrow was negatively related to residual tree density in 1997, while no species showed this relationship in 1995. The increase in negative association with residual tree density is likely due to the influx of open-area birds into logged sites between 1995 and 1997. The decrease in positive association with high residual tree density cannot be explained by a loss of common forest species because there was no difference in total abundance of these birds between years. Instead, regeneration may have reduced differences in habitat quality in the first three years post-logging; birds responding positively to high levels of residual tree density immediately following the harvest spread out to all logged areas regardless of residual tree density by the third year. Species associated with shrubs, such as the Mourning Warbler (S. Song unpublished data) may have responded more to shrub or sapling cover than to residual tree density and thus regeneration may have resulted in all logged sites having equal habitat quality.

These results are consistent with several studies that found little effect of residual tree retention (Scott and Gottfried 1983, Medin and Booth 1989) and inconsistent with several other studies which found the opposite (Webb et al. 1977, Freedman et al. 1981, Merrill et al. 1998). All the studies that found significant effects of retention of residual trees considered either strips, larger clumps of residual trees, or higher percentages of residual tree retention than those considered here, all three of which may provide better habitat for forest birds (Webb et al. 1977, Freedman et al. 1981, Merrill et al. 1998). Based on their finding that strip or shelterwood logging did not negatively impact forest birds in Ponderosa pine but heavy thinning was detrimental, Szaro and Balda (1979) recommended removing no more that 45% of the trees from mixed conifer forests. Residual tree retention in logged sites in my study ranged from 11% to 39% with a mean of 25.9%.

These data are contrary to the predictions of Norton and Hannon (1997). Norton and Hannon foresaw a more rapid increase over time in abundances of common forest birds in sites with high densities of residual trees than in sites with low densities of residual trees. They feared that their two-season study would under-estimate the benefits

of sites with high densities of residual trees and that further study would reveal a widening of the gap between sites with high and sites with low densities of residual trees in terms of forest bird abundances.

Although my findings indicate a pattern opposite to that predicted by Norton and Hannon (1997), re-visiting the study at a later date might show greater benefits of leaving high densities of residual trees in logged sites. One of the possible long-term benefits of this approach may be improved conifer regeneration (Bella and Gál 1996). When an aspen-spruce mixed-wood stand is logged, the aspen component regenerates rapidly thanks to its ability to sucker quickly from existing shoots under high light conditions (Peterson and Peterson 1992). The shade-tolerant spruce grows far more slowly and prefers the shelter of other trees (Bella and Gál 1996). Leaving high densities of residual trees might provide spruce saplings with more of the shelter they favour and reduce the competition from the quickly regenerating aspen and poplar in this shelter. A few decades after logging, sites with high residual tree density may have a greater spruce component than those with low residual tree density. Rose and Muir (1997) found that retention of greater than 15 trees/ha improved regeneration of shade tolerant species in the western hemlock – Douglas fir forest of the western Cascades. Forest species such as the Black-throated Green Warbler may be dependent on the spruce component of the mixed-wood (R. Tittler unpublished data, S. Song unpublished data) and therefore might benefit from high residual tree retention in the future.

Furthermore, residual trees may provide structural and age diversity to the regenerating stands, and this, in turn, may benefit forest birds over the long term (Rose and Muir 1997). For example, some of the residual trees will become snags, and these will provide nesting sites for cavity nesters and foraging sites for bark gleaners (Niemi and Hanowski 1984).

2.4.3 *Role of Nesting Guild, Foraging Guild, and Migratory Strategy*

Analysis of nesting guild, foraging guild, and migratory strategy did not indicate different patterns of response to logging or retention of residual trees among life history groups. Identified species of concern included species from all nesting and foraging guilds and of all migratory strategies in 1997, and all but the rare cavity nesters were represented among species recorded at lower abundances in logged than forested sites in

1995. As predicted, species increasing with increasing residual tree density in 1995 and 1997 were shrub or tree nesters, but numbers were low and no significant effect was detected. Species increasing with increasing residual tree density in 1995 and 1997 were also all aerial or foliage gleaners and neotropical migrants, but again numbers were low and no significant effect was detected. Identified open-area species included birds of all foraging guilds except the rare bark gleaners and of all migratory strategies except the rare residents. These results imply that a focus on individual species is more appropriate than a classification of species by guild.

2.4.4 *Vegetation Characteristics and Songbird Community*

Basal area of conifer, grass cover, and number of small deciduous trees were important in explaining songbird community composition in logged sites. However, since small samples are not likely to be representative of true patterns (Zar 1984), I only included species abundant in logged sites in these analyses. Variables such as number of snags or shrub cover may be important to forest birds (Merrill et al. 1998, Niemi and Hanowski 1984) but levels may not have been high enough in the logged sites studied to result in high abundances of the birds for which they are important. For example, if there had been more shrub cover in logged sites, American Redstarts might have been abundant enough to be included in the analysis and the RDA might have indicated shrub cover as an important predictor of the songbird community in logged sites. Based on the limited range of each environmental variable measured in logged sites, I can only conclude that open-area species were associated with grass and some of the forest species that were abundant in logged sites were associated with small deciduous trees or conifer. Since none of these variables were highly correlated with residual tree density, they should be considered apart from residual tree retention in managing for songbird conservation.

2.4.5 *Species in Trouble Across North America*

Two of the identified species of concern are declining significantly across North America (Sauer et al. 1997). The Canada Warbler declined between 1966 and 1996 and the Swainson's Thrush between 1980 and 1996. The Swainson's Thrush was recorded in logged sites in both the first and third year post-logging but abundances were low and those individuals recorded in logged sites may not have been breeding in these areas.

Even if individuals were breeding, abundances would likely be insufficient to sustain viable populations. Furthermore, Swainson's thrushes did not respond to increasing residual tree density in logged sites. The Canada Warbler was not recorded in logged sites in either post-logging year, regardless of residual tree density. Both species prefer old-growth stands in the boreal mixed-wood (Schieck and Nietfeld 1995). Maintenance of old growth reserves may be crucial to the conservation of these two species in Alberta.

Abundances of four other identified common forest species have also been declining across North America (Sauer et al. 1997). The Least Flycatcher and White-throated Sparrow declined between 1966 and 1996, while the Rose-breasted Grosbeak and Mourning Warbler declined between 1980 and 1996. The White-throated Sparrow and the Mourning Warbler were abundant in logged sites: by the third year post-logging, abundances of both species were higher in logged than forested sites, and the species were thus defined as open-area species. The Least Flycatcher was present in logged and forested sites alike and was associated with small deciduous trees. Since small deciduous trees will likely be abundant in the logged landscape due to the rapid regeneration of aspen, conservation of these three species may not be difficult in a logged boreal mixed-wood.

Conservation of the Rose-breasted Grosbeak is less certain. This species was recorded at lower abundances in logged than forested sites in the first year post-logging but showed no difference by the third year post-logging. This may indicate that the species was only initially negatively impacted by logging. However, due to the relatively large territory size of this species (S. Song unpublished data), it is particularly difficult to judge whether Rose-breasted Grosbeaks are actually nesting in logged sites. The Rose-breasted Grosbeak has been classified as preferring 20-30 year old stands (Schieck and Neitfeld 1995) but we do not know whether stands younger than 20 years provide suitable nesting habitat. Future research is necessary to determine whether this species is dependent on adjacent older forested stands for nesting sites.

Apart from the White-throated Sparrow and the Mourning Warbler, three other open-area species have been declining across North America (Sauer et al. 1997). The Clay-coloured Sparrow and the Song Sparrow declined between 1966 and 1990, and the Common Yellowthroat, between 1966 and 1996. All three species were recorded at

relatively high abundances in logged sites regardless of residual tree density and therefore may be positively rather than negatively affected by logging in the boreal mixed-wood.

2.4.6 *Recommendations for Future Research*

As mentioned above, this study is incomplete without a component on reproductive activity and success. I have addressed the issue of nest predation in a companion paper based on an artificial nest experiment (Chapter 3), but specific information on nesting and breeding success is lacking. Logged sites with high densities of residual trees may host nesting forest birds while those with low densities of residual trees only provide singing posts. Forest birds nesting in sites with low densities of residual trees may have to maintain larger territories and may therefore experience lower breeding success. It is difficult to draw conclusions about the value of residual tree retention without insight into these issues.

It would also be useful to expand this study to include a broader range of residual tree retention. The site with the lowest density of residual trees studied had a mean of 10 trees/ha, more than is being left in many logged stands (Alberta Pacific Forest Industries Inc. 1996, Weyerhaeuser Canada Ltd. 1998). For management purposes, it would be useful to investigate the effects of retention of very low and very high densities of residual trees on songbirds. From a biological perspective, it would also be interesting to examine the effects of retention of very high densities of residual trees; there may be a threshold level at which the community in logged sites becomes more similar to the community in forested sites.

I also recommend that this study be continued to investigate the possible benefits of high densities of residual trees in improving regeneration in logged sites and to examine changes in songbird community in logged sites to see when and if species of concern move into the area. Research indicates that community change may be rapid for the first few decades following logging (Thiollay 1992, Welsh 1987) and this is supported by my data.

Specifically, I recommend that all sites be censused in the year before and the year after the second pass, at which time the sites will be nine and ten years of age. This long-term research should also include sites with higher and lower residual tree retention than those studied here. I predict that conifer regeneration and snag production will be

facilitated by retention of high densities of residual trees in cutblocks. However, since most of the species of concern are associated with old-growth forest (Schieck and Nietfeld 1995), it is unlikely that regeneration will be sufficient to maintain high levels of forest songbirds in these ten-year-old stands after the second pass, regardless of residual tree retention.

2.4.7 *Conclusion*

Contrary to Norton and Hannon's original findings (1997), this continuation of their study indicates that few species benefit more from retention of high densities of residual trees than from retention of low densities of residual trees in logged sites. Fewer species of concern were recorded in logged sites than in forested sites regardless of varying densities of residual trees in logged sites. However, I cannot draw conclusions about the effects of leaving densities of residual trees lower than the lowest level included in this study (10 trees/ha). Since over 70% of the identified common forest birds were shrub or tree nesters, retention of many forest species might be impossible in logged sites with no residual trees. Pending further research, these results imply that it may be more beneficial to the conservation of forest songbirds to set aside more old growth as protected areas than to leave densities of residual trees higher than 10 trees/ha in logged sites. However, if leaving high densities of residual trees improves conifer regeneration and provides snags and structural diversity to the regenerating stand, longer term research may indicate that this system is beneficial to forest songbirds. Considering the changes in songbird community and in the effect of residual tree density on this community in the first three years following logging, it is evident that long-term research is crucial to resolve this issue.

Table 2.1. Comparisons of mean abundances (per site) of common forest birds and open-area birds in logged and forested sites in 1995 and 1997. Means were compared between years using paired t-tests (PT) and between treatments within years using t-tests for independent samples (IT). In both cases, randomized t-tests (RT) were performed if power was low (< 0.65, $\alpha = 0.10$). No test statistics are available for randomized t-tests. Standard errors follow means in parentheses and results of significant tests ($p < 0.10$) are presented in bold. Group 1 = forested or 1995 data, Group 2 = logged or 1997 data.

		Group 1		Group 2				
Community	**Comparison**	**Mean**	**Sites (N)**	**Mean**	**Sites (N)**	**Test**	**T-Statistic**	**P-Value**
Forest	**Forested vs Logged '95**	**13.1 (1.38)**	**3**	**6.3 (1.05)**	**9**	**IT**	**3.47**	**0.006**
Forest	**Forested vs Logged'97**	**8.7 (1.12)**	**6**	**5.9 (0.46)**	**12**	**IT**	**3.87**	**0.001**
Forest	'95 vs '97 Logged Sites	6.3 (1.05)	9	6.2 (0.54)	9	RT		0.784
Forest	'95 vs '97 Forested Sites	13.1 (1.38)	3	9.6 (0.25)	3	PT	2.49	0.131
Open-Area	Forested vs Logged '95	3.6 (0.53)	3	3.4 (0.36)	9	RT		0.812
Open-Area	**Forested vs Logged '97**	**2.0 (0.46)**	**6**	**6.4 (0.32)**	**12**	**IT**	**-6.35**	**0**
Open-Area	**'95 vs '97 Logged Sites**	**3.4 (0.36)**	**9**	**6.1 (0.39)**	**9**	**PT**	**-5.03**	**0.001**
Open-Area	'95 vs '97 Forested Sites	3.6 (0.53)	3	2.5 (0.27)	3	RT		0.118

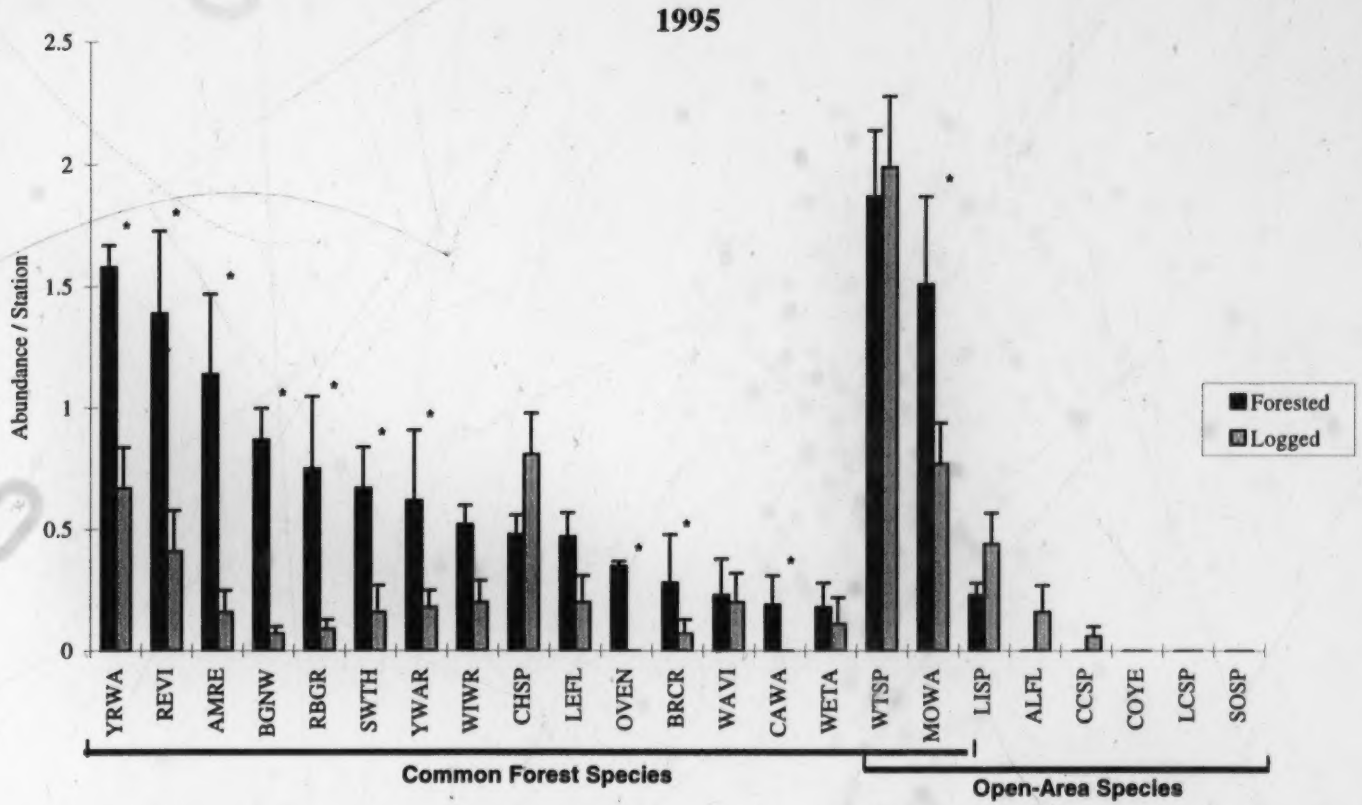

Figure 2.1. Mean abundance of common forest and open-area species in logged (N = 9) and forested sites (N = 3) in 1995. Species demonstrating significant differences in abundance ($p < 0.10$) are marked (*). Common forest species are defined as species abundant before logging. Open-area species are defined as those recorded at significantly lower abundances in forested than in logged sites. Refer to Appendix 2.2 for full species name Error bars represent standard errors of means.

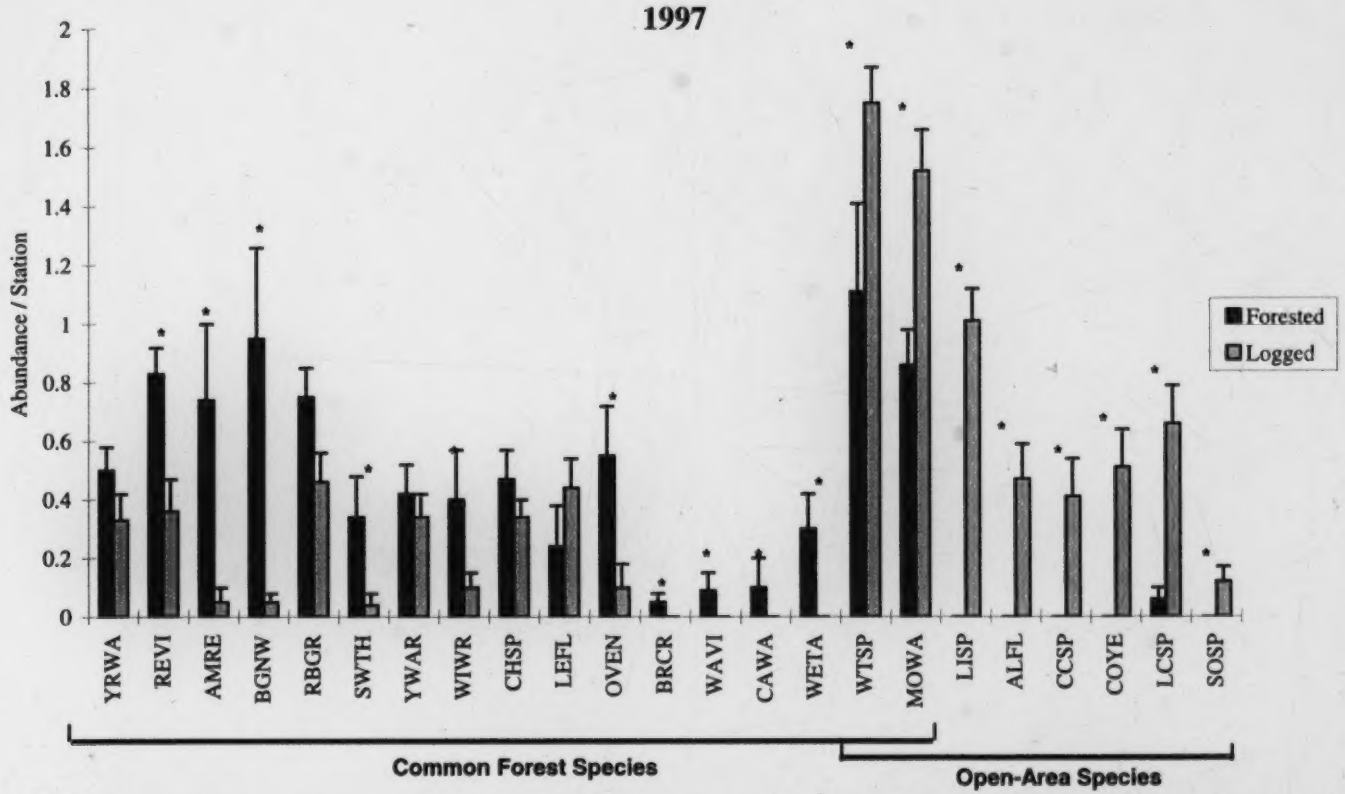

Figure 2.2. Mean abundance of common forest and open-area species in logged (N = 12) and forested sites (N = 6) in 1997. Species demonstrating significant differences in abundance ($p < 0.10$) are marked (*). Common forest species are defined as species abundant before logging. Open-area species are defined as those recorded at significantly lower abundances in forested than in logged sites. Species of concern are defined as common for species recorded at significantly lower abundances in logged than in forested sites. Refer to Appendix 2.2 for full species names. Error bars represent standard errors of means.

Table 2.2. Turnover of common forest and open-area communities between the first and third year post-logging in logged and forested sites. Turnover was calculated in terms of species presence (Jaccard Index) and abundance (Phi-Square Index). Indices vary from 0 to 1, with 1 being the highest possible turnover (no similarity) and 0 the lowest possible turnover (complete similarity). Turnover in logged and forested sites was compared with t-tests for independent samples (IT), Mann-Whitney U tests (MW), or randomized t-tests (RT), depending on power, normality, and homogeneity of variance. Standard errors follow means in parentheses and results of significant tests ($p < 0.10$) are presented in bold. No test statistics are available for randomized t-tests.

Community	Index	Years	Mean Logged	Mean Forested	Test	Test-Statistic	P-Value
Common Forest	**Jaccard**	**1994-1995**	**0.60 (0.07)**	**0.25 (0.07)**	**IT**	**t = -2.589**	**0.027**
Common Forest	**Jaccard**	**1994-1997**	**0.52 (0.06)**	**0.29 (0.13)**	**RT**		**0.082**
Common Forest	**Jaccard**	**1995-1997**	**0.61 (0.04)**	**0.34 (0.16)**	**MW**	**U = 4.00**	**0.100**
Common Forest	**Phi-Square**	**1994-1995**	**0.50 (0.03)**	**0.38 (0.01)**	**RT**		**0.081**
Common Forest	Phi-Square	1994-1997	0.54 (0.05)	0.38 (0.08)	RT		0.181
Common Forest	**Phi-Square**	**1995-1997**	**0.57 (0.03)**	**0.45 (0.08)**	**RT**		**0.098**
Open-Area	**Jaccard**	**1994-1995**	**0.22 (0.15)**	**0 (0)**	**RT**		**0.052**
Open-Area	**Jaccard**	**1994-1997**	**0.20 (0.08)**	**0 (0)**	**RT**		**0.099**
Open-Area	Jaccard	1995-1997	0.05 (0.03)	0 (0)	RT		0.266
Open-Area	Phi-Square	1994-1995	0	0 (0)	none	-------	-------
Open-Area	**Phi-Square**	**1994-1997**	**0.47 (0.13)**	**0 (0)**	**RT**		**0.053**
Open-Area	Phi-Square	1995-1997	0.09 (0.06)	0.67 (0.33)	MW	U = 5.50	0.145

Table 2.3. Linear regressions of abundances of common forest (f) and open-area (o) species vs. residual tree density in logged sites the year after (1995) and three years after logging (1997). A positive slope (*B*) indicates an increase in abundance with increasing tree density, and a negative slope, the opposite. Tests with significant p-values ($p < 0.10$) are presented in bold.

	1995				1997			
Species	**R^2**	***B***	**F-Statistic**	**P-Value**	**R^2**	***B***	**F-Statistic**	**P-Value**
American Redstart [f]	**0.450**	**0.671**	**5.72**	**0.048**	0.008	-0.089	0.08	0.682
Black-Throated Green Warbler [f]	0.021	-0.144	0.14	0.712	0.102	-0.32	1.15	0.290
Brown Creeper [f]	0.004	-0.066	0.03	0.867	-------	-------	-------	-------
Chipping Sparrow [f]	0.146	0.382	1.19	0.310	0.144	0.379	1.65	0.238
Least Flycatcher [f]	0.263	0.513	2.51	0.158	0.165	0.406	1.96	0.195
Mourning Warbler [f], [o]	**0.489**	**0.699**	**6.69**	**0.036**	0.028	0.167	0.28	0.586
Ovenbird [f]	-------	-------	-------	-------	0.179	0.423	2.2	0.211
Rose-Breasted Grosbeak [f]	0.023	0.151	0.16	0.698	0.036	-0.189	0.36	0.552
Red-Eyed Vireo [f]	0.018	0.133	0.13	0.734	0.001	0.036	0.01	0.948
Swainson's Thrush [f]	**0.484**	**0.696**	**6.57**	**0.037**	0.255	0.505	3.43	0.16
Warbling Vireo [f]	0.001	0.038	0.01	0.665	-------	-------	-------	-------
Western Tanager [f]	0.305	0.552	3.07	0.123	-------	-------	-------	-------
Winter Wren [f]	0.180	0.424	1.54	0.256	0.207	0.455	2.59	0.135
White-Throated Sparrow [f], [o]	0	0.002	0	0.996	0.046	0.215	0.48	0.519
Yellow Warbler [f]	**0.453**	**0.673**	**5.79**	**0.047**	0.001	-0.023	0.01	0.939
Yellow-Rumped Warbler [f]	0.067	0.259	0.5	0.501	**0.396**	**0.629**	**6.55**	**0.029**
Alder Flycatcher [o]	0.182	0.433	1.61	0.245	0.195	-0.442	2.44	0.156
Clay-Coloured Sparrow [o]	0.016	-0.125	0.12	0.750	0.114	-0.337	1.3	0.269
Common Yellowthroat [o]	-------	-------	-------	-------	0.213	-0.461	2.71	0.135
LeConte's Sparrow [o]	-------	-------	-------	-------	0.15	-0.387	1.78	0.231
Lincoln Sparrow [o]	0.125	-0.354	1.01	0.351	**0.374**	**-0.611**	**5.97**	**0.035**
Song Sparrow [o]	-------	-------	-------	-------	0.135	-0.367	1.53	0.259
Total Common Forest Species	0.317	0.563	3.25	0.125	0.115	0.334	2.97	0.121
Total Open-Area Species	0.110	0.337	0.09	0.768	**0.240**	**-0.489**	**3.39**	**0.086**

Table 2.4. Results of linear regressions of density of residual trees vs. turnover pre- to post-logging measured by similarity (Jaccard) and dissimilarity (Phi-Square) indices. Indices compare turnover in the common forest species community in each logged site between 1994 and 1995 and between 1994 and 1997 in terms of species presence (Jaccard) and abundance (Phi-Square). Jaccard indices have been subtracted from 1 so that 1 represents the highest (no similarity) and 0 the lowest turnover (complete similarity) for both indices. Since power was low (<0.65 at $\alpha = 0.10$) for all regressions, presented p-values are based on randomized linear regressions.

Index	Comparison	Equation	R^2	F-Statistic	P-Value
Jaccard	1994 vs 1995	$y = 0.404 + 1.016x$	0.023	1.620	0.239
Jaccard	1994 vs 1997	$y = 0.629 + 1.014x$	0.038	0.020	0.884
Phi-Square	1994 vs 1995	$y = 1.197 + 0.992x$	0.038	0.290	0.611
Phi-Square	1994 vs 1997	$y = 0.579 + 1.014x$	0.046	0.420	0.551

Table 2.5. Comparison of mean turnover in common forest and open-area communities. Indices compare turnover in common forest species community in each logged site between pre- and post-logging (1994 to 1995 and 1994 to 1997) in terms of species presence (Jaccard) and abundance (Phi-Square). Jaccard indices have been subtracted from 1 so that 1 represents the highest (no similarity) and 0 the lowest turnover (complete similarity) for both indices. Means were compared using Wilcoxon paired-sample tests (WX) if power was high (≥ 0.65 at $\alpha = 0.10$), or using randomized t-tests (RT) if power was low (< 0.65 at $\alpha = 0.10$). Randomized t-tests do not provide test statistics. Tests with significant p-values ($p < 0.10$) are presented in bold.

Community	Index	Mean 1994-1995	Mean 1994-1997	Test	Test-Statistic	P-Value
Common Forest	Jaccard	0.78 (0.15)	0.80 (0.08)	RT		0.380
Common Forest	Phi-Square	0	0.47 (0.13)	RT		0.592
Open-Area	Jaccard	0.60 (0.07)	0.52 (0.06)	RT		0.867
Open-Area	**Phi-Square**	**0.50 (0.03)**	**0.54 (0.05)**	**WX**	**Z = -2.366**	**0.018**

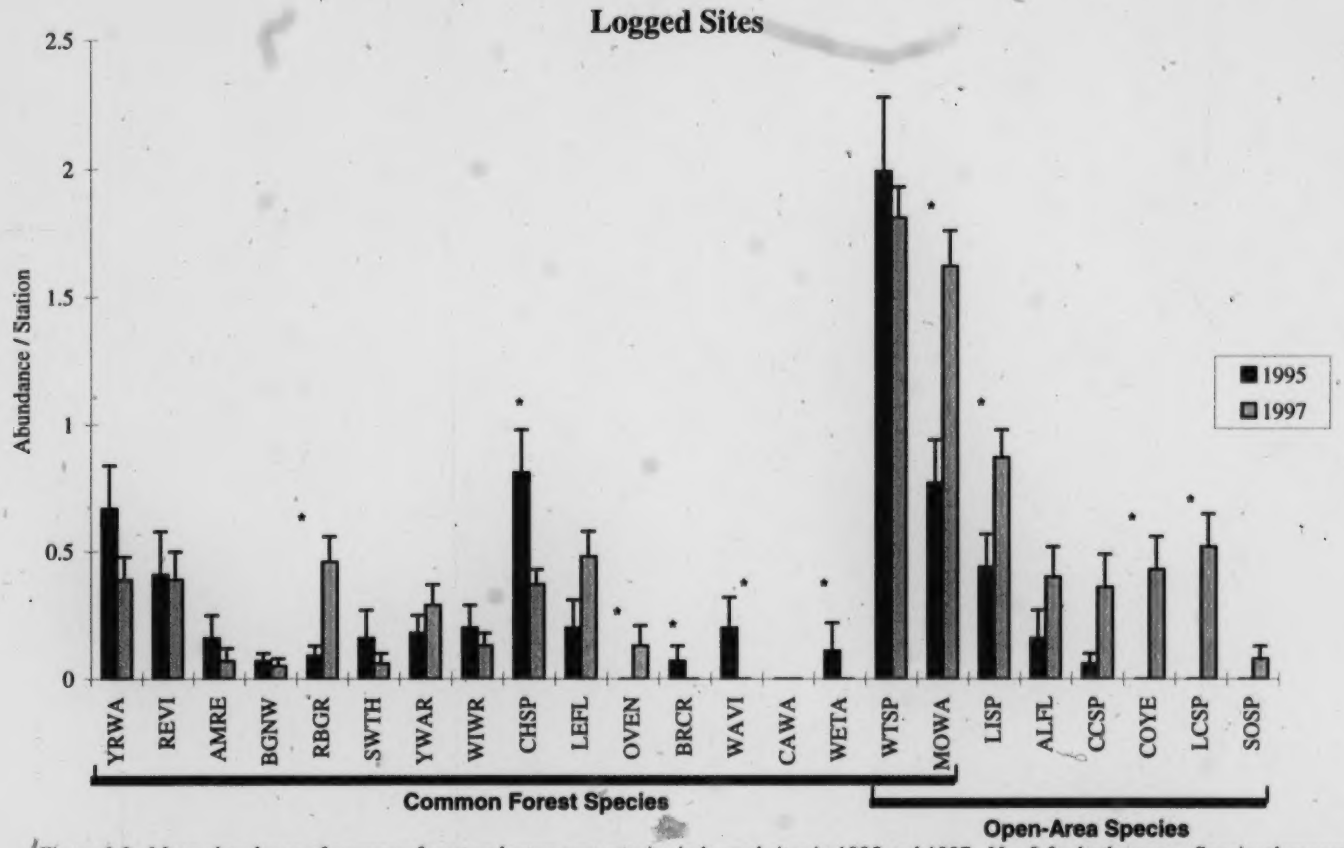

Figure 2.3. Mean abundance of common forest and open-area species in logged sites in 1995 and 1997. N = 9 for both years. Species demonstrating significant differences in abundance ($p < 0.10$) are marked (*). Common forest species are defined as species abundant before logging. Open-area species are defined as those recorded at significantly lower abundances in forested than in logged sites. Refer to Appendix 2.2 for full species names. Error bars represent standard errors of means.

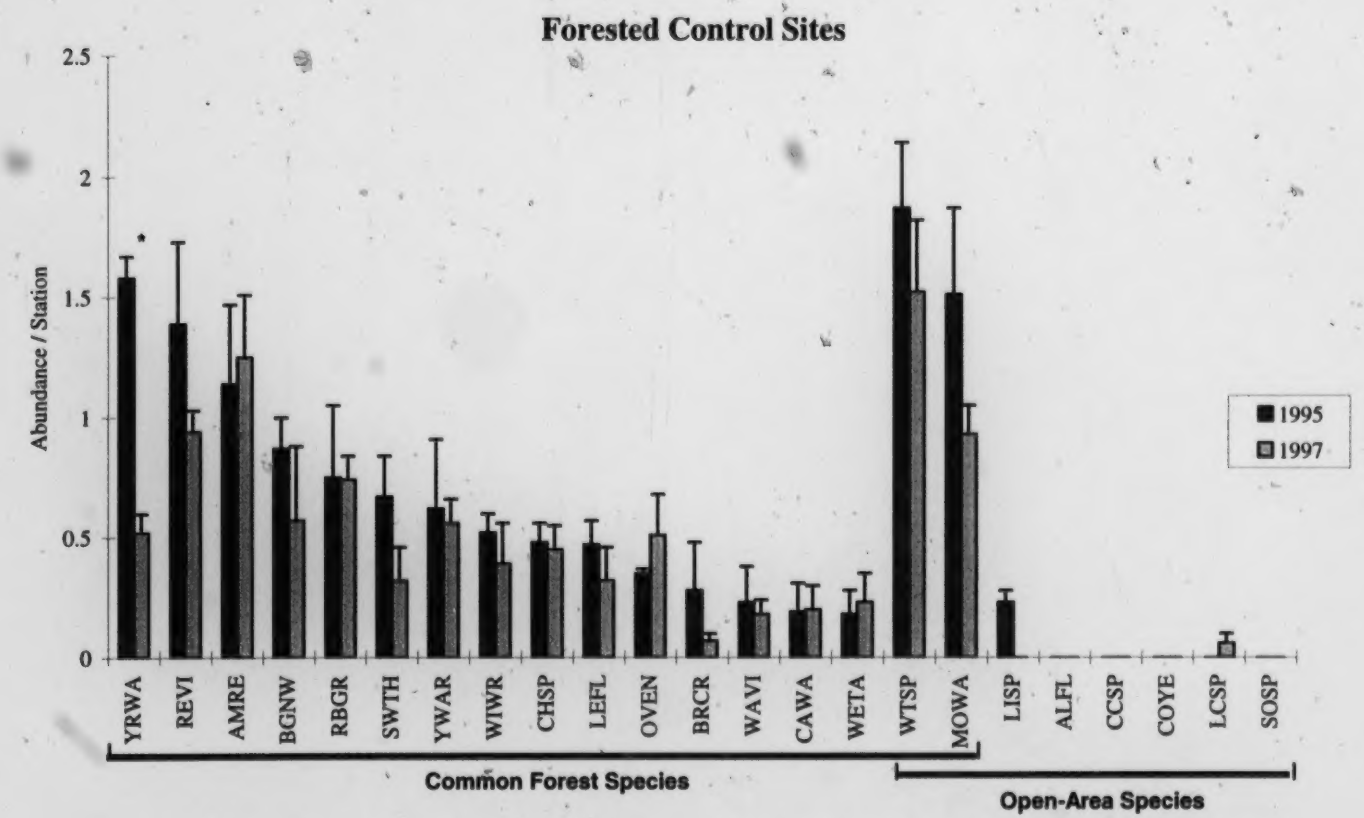

Figure 2.4. Mean abundance of common forest and open-area species in forested sites in 1995 and 1997. N = 3 for both years. Species demonstrating significant differences in abundance ($p < 0.10$) are marked (*). Common forest species are defined as species abundant before logging. Open-area species are defined as those recorded at significantly lower abundances in forested than in logged sites. Refer to Appendix 2.2 for full species names. Error bars represent standard errors of means.

Table 2.6. Results of log-likelihood analyses investigating whether foraging guild had an effect on (a) which of the common forest species were recorded at lower abundances in logged than forested sites ("Species of Concern"), (b) which of the common forest species increased with increasing residual tree density ("Residual Species"), and (c) which of all species were recorded at higher abundances in logged than in forested sites ("Open-Area Species"). The number of species in each guild are presented as well as the χ^2 values and p-values. Data are not presented for open-area birds in 1995 because no birds were recorded at higher abundances in logged than in forested sites in this first year after logging. Similarly, data are not presented on which species increased with increasing residual tree density in 1997 because only one species fit this description.

Year	Group of Birds	Aerial	Foliage	Bark	Ground	χ^2	P-Value
1995	Species of Concern	3	6	1	1	4.080	0.264
	Common Forest Species	4	8	1	4		
1997	Species of Concern	3	4	1	2	1.901	0.551
	Common Forest Species	4	8	1	4		
1995	Residual Species	1	2	0	5	3.467	0.315
	Common Forest Species	4	8	1	4		
1997	Open-Area Species	1	2	0	5	2.877	0.371
	All Species	5	13	3	15		

Table 2.7. Results of log-likelihood analyses investigating whether nesting guild had an effect on (a) which of the common forest species were recorded at lower abundances in logged than forested sites ("Species of Concern"), (b) which of the common forest species increased with increasing residual tree density ("Residual Species"), and (c) which of all species were recorded at higher abundances in logged than in forested sites ("Open-Area Species"). The number of species in each guild are presented as well as the χ^2 values and p-values. Data are not presented for open-area birds in 1995 because no birds were recorded at higher abundances in logged than in forested sites in this first year after logging. Similarly, data are not presented on which species increased with increasing residual tree density in 1997 because only one species fit this description.

Year	Group of Birds	Shrub/Tree	Ground	Cavity	χ^2	P-Value
1995	Species of Concern	8	3	0	2.300	0.416
	Common Forest Species	12	4	1		
1997	Species of Concern	7	2	1	1.189	0.659
	Common Forest Species	12	4	1		
1995	Residual Species	3	1	0	0.555	0.773
	Common Forest Species	12	4	1		
1997	Open-Area Species	6	2	0	4.008	0.249
	All Species	17	16	3		

Table 2.8. Results of log-likelihood analyses investigating whether migratory strategy had an effect on (a) which of the common forest species were recorded at lower abundances in logged than forested sites ("Species of Concern"), (b) which of the common forest species increased with increasing residual tree density ("Residual Species"), and (c) which of all species were recorded at higher abundances in logged than in forested sites ("Open-Area Species"). The number of species in each guild are presented as well as the χ^2 values and the p-values. Data are not presented for open-area birds in 1995 because no birds were recorded at higher abundances in logged than in forested sites in this first year after logging. Similarly, data are not presented on which species increased with increasing residual tree density in 1997 because only one species fit this description.

Year	Group of Birds	Neotropical Migrants	Short-Distance Migrants	Residents	χ^2	P-Value
1995	Species of Concern	9	1	1	2.207	0.418
	Common Forest Species	13	3	1		
1997	Species of Concern	8	1	1	1.892	0.462
	Common Forest Species	13	3	1		
1995	Residual Species	4	0	0	2.502	0.356
	Common Forest Species	13	3	1		
1997	Open-Area Species	4	4	0	2.464	0.382
	All Species	23	11	2		

Table 2.9. Summary statistics from redundancy analysis (RDA) showing the coefficients and correlations of the environmental variables with the first two RDA axes. Significant coefficients ($p < 0.05$) are marked (*). Measured means and ranges are also presented. Conifer basal area (BA) and number of small deciduous trees are means per vegetation plot (0.04 ha) and grass is a mean percentage cover per $1m^2$ quadrat.

			Canonical Coefficients		Canonical Correlations	
Variable	Mean	Range	Axis 1	Axis 2	Axis 1	Axis 2
Conifer BA (cm^2)	143.6	0-468.7	-0.8393 *	-0.6781 *	-0.4341	-0.6727
Small Deciduous Trees (#)	1.2	0-5.2	-1.2270 *	0.2471	-0.5684	0.6616
Grass (%)	39.5	8.1-50.8	-0.4376	-0.4209	0.3656	-0.5582

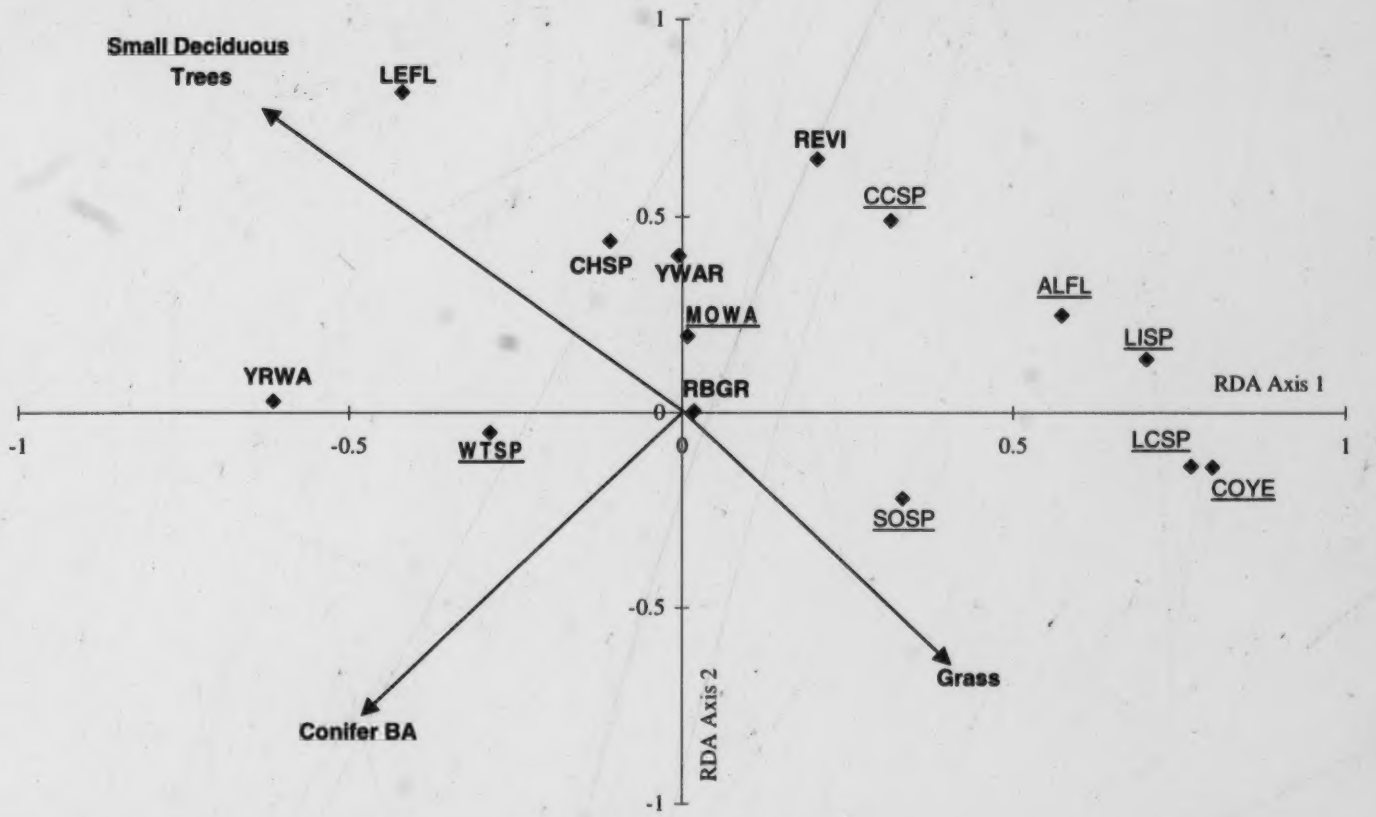

Figure 2.5. Biplot of the first two RDA axes showing species and environmental scores. Refer to Appendix 2.2 for full species names. Open-area species are underlined and forest species are presented in bold. Only logged sites and species with total abundances greater than 5 were included. Eigenvalues are 0.240 and 0.127 for the first and second axis respectively.

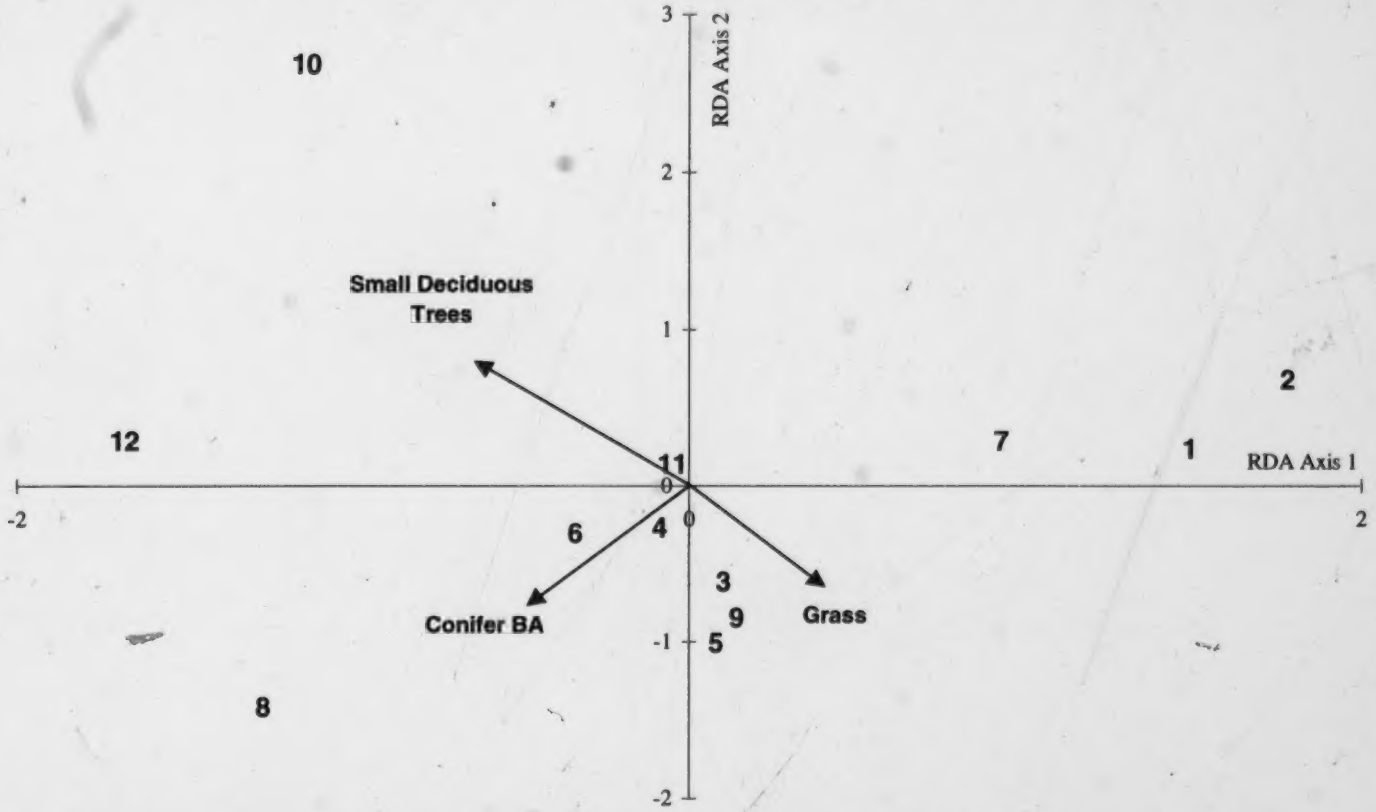

Figure 2.6. Biplot of first two RDA axes showing sites and environmental scores. Numbers represent logged sites in order from the lowest residual (1) to the highest residual (12). Only logged sites and species with total abundances greater than 5 were included. Eigenvalues are 0.240 and 0.127 for the first and second axis respectively.

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CHAPTER 3

NEST PREDATION AND RESIDUAL TREE RETENTION IN ALBERTA'S BOREAL MIXED-WOOD FOREST

3.1 Introduction

Nest predation is a major factor in reducing productivity of birds (Ricklefs 1969). In agricultural and logged landscapes, predation at forest edges is often higher than in the forest interior (Gates and Gysel 1978, Robbins 1980, Ambuel and Temple 1983, Andrén et al. 1985, Wilcove 1985, Andrén and Angelstam 1988, Johnson and Temple 1990, Vander Haegen and DeGraaf 1996). In a time when habitat fragmentation is rampant and many songbird populations are declining (Wilcove and Whitcomb 1983, Terborgh 1989, Robbins et al. 1989, Robinson 1997, Sauer et al. 1997), concern over the negative effects of nest predation is high, as evidenced by the plethora of recent studies on the issue (for reviews see Paton 1994 and Andrén 1995). Along with habitat loss, nest predation may be a major cause of declines in songbird numbers (Wilcove 1985, Wilcove et al. 1986, Terborgh 1989, Askins et al. 1990).

In the boreal mixed-wood of Alberta, forests are being rapidly fragmented and forest edges created by logging. A total of 195 662 km^2 are designated to be logged in the next few decades (D. Price, Alberta Environmental Protection, pers. comm.). Hardwood forests are being harvested in a two- to three-pass system that creates a patchwork of logged stands across the landscape. Most logged stands are 10 to 60 ha in size, resulting in the creation of thousands of kilometers of cutblock-forest edge.

Norton and Hannon (1997) investigated the conservation potential of leaving high densities of residual trees in logged mixed-wood stands in Alberta's boreal forest. They found higher songbird species richness and abundance in high residual ("partial-cut") than in low residual ("clearcut") sites in the first year after logging. Many of the forest species that disappeared from clearcuts were recorded at low abundances in partial-cuts. Norton and Hannon concluded that it may be beneficial to songbirds to leave high levels of residual trees in logged sites. Other studies also indicate the potential benefits of residual tree retention (Webb et al. 1977, Merrill et al. 1998). However, none of these studies have investigated the possibility that sites with high residual tree retention might be sources of high nest predation. If birds were nesting in logged sites with high

densities of residual trees or in stands adjacent to these sites but experiencing low productivity, leaving high densities of residual trees in logged sites might not be beneficial to the conservation of forest birds.

Several hypotheses have been proposed to explain higher rates of nest predation in stands adjacent to clearings than in forest interiors and some of these may also be applicable to predation in clumps of residual trees. First, the density-dependent nest predation hypothesis proposes that densities of nesting birds are higher along edges than in interior forest due to unique vegetation characteristics at the edge, and that predators respond to these increased densities by concentrating foraging efforts in these areas (Gates and Gysel 1978). This hypothesis might also apply to predation in residual tree clumps if these were large enough to support high densities of nesting birds. Second, predators may use forest edges or adjacent clearings as travel corridors, resulting in higher predator abundances in these areas than in interior forest (Bider 1968). Third, the abundance and richness of predators in logged sites may be higher than in forest due to habitat differences and thus logged sites may serve as predator sources for adjacent forest edges and for residual tree clumps (Andrén and Angelstam 1988, Andrén 1995). Finally, the presence of clearings may facilitate predator foraging ability in residual tree clumps and forest edges by increasing visibility of nests.

In the boreal mixed-wood forest, elevated levels of predation have not been recorded in stands adjacent to logged sites with few residual trees (clearcuts) (Cotterill 1996, Bayne and Hobson 1997), nor are bird densities along clearcut edges higher than in the forest interior after the first year post-logging (Song and Hannon in prep.). However, retention of high densities of residual trees could change conditions for nesting birds and predators in residual tree clumps and in forested stands adjacent to logged sites. Predation may be facilitated for visually oriented avian predators because residual trees provide perches from which avian predators may be able to see nests (Yahner and Wright 1985). Nesting birds may use residual trees as songposts and nest in adjacent forested stands (Lambert 1998), resulting in high nesting densities along the forest edge and thus concentrated predator foraging. Finally, forest predators may be more likely to travel between clumps of residual trees than across large forest openings such as clearcuts.

Among the nest predators identified in the boreal mixed-wood by Cotterill (1996),

Bayne and Hobson (1997), and Hannon and Cotterill (1998) are corvids such as Grey Jays (*Perisoreus canadensis*), American Crows (*Corvus brachyrhyncos*), and Common Ravens (*C. corax*), and mammals such as red squirrels (*Tamiascurus hudsonicus*). Red squirrels have been found to avoid clearcuts in the Douglas fir stands of Oregon (Gashwiler 1970). Murid rodents ("murids") have also been identified as predators in the boreal mixed-wood but red-backed voles (*Clethrionymus gapperi*) have not been distinguished from deer mice (*Peromyscus maniculatus*) (Cotterill 1996, Bayne and Hobson 1997, Hannon and Cotterill 1998). Both species have been identified as nest predators in other systems (Maxson and Oring 1978, Fenski-Crawford and Niemi 1997). Research in aspen stands in Minnesota and Michigan indicates that red-backed voles may avoid recent clearcuts (Probst and Ragstad 1987), while deer mice are abundant in clearcuts and forested aspen stands in Minnesota and Michigan (Probst and Ragstad 1987) and in the boreal mixed-wood forest of Alberta (Weaver 1996). Thus red-backed voles may be affected but deer mice will likely not be affected by retention of residual trees. Another predator identified in the boreal mixed-wood is the House Wren (*Troglodytes aedon*) (Hannon and Cotterill 1998), which is abundant in logged sites regardless of residual tree retention (Chapter 2).

To investigate whether residual tree retention affected predation, I performed an artificial nest experiment in residual tree clumps in logged sites and in forested stands adjacent to logged sites with varying densities of residual trees. I predicted that avian and red squirrel predation would (a) be higher in residual clumps in logged sites with high densities of residual trees than in those with low densities of residual trees and (b) be higher in stands adjacent to logged sites with high densities of residual trees than in those adjacent to logged sites with low densities of residual trees. Since red-backed vole predation was not distinguishable from deer mouse predation in this study, I also predicted that murid (vole and mouse) predation would be higher in and adjacent to logged sites with high rather than low densities of residual trees, assuming that red-backed vole predation would account for a sizable portion of this group.

3.2 Methods

3.2.1 *Study Area and Experimental Set-Up*

This study was carried out in an area of approximately 10 by 15 km in the boreal

mixed-wood forest of Alberta (55°15'N, 113° 35"W). The boreal mixed-wood forest is dominated by a combination of hardwoods [trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifer*)] and softwoods [white spruce (*Picea glauca*), black spruce (*P. mariana*), and jack pine (*Pinus banksiana*)] (Rowe 1972). Although the forest is naturally fire-disturbed, it is now the focus of extensive logging and gas and oil activity, resulting in a landscape mosaic of cutblocks, seismic lines, pipelines, roads, and clearings for well-heads.

In the winter of 1994-95, 12 of 18 study sites were logged. The remaining six sites were left forested and served as control sites. This study was performed in 1997, three years after logging. All sites were aspen-dominated mixed-wood stands greater than 130 years old before logging. Logging was done using feller-bunchers, skidders, and role-stroke delimbers (Norton and Hannon 1997). Logging operators were instructed to leave residual tree clumps and individual trees throughout the cutblocks, regardless of timber type, to establish six "partial-cuts", three with approximately 30% residual tree retention ("low-residual partial-cuts") and three with 50% residual tree retention ("high-residual partial-cuts"). All sites were between 12 and 35 ha in size and sizes were stratified across the initial four treatments (clearcuts, low-residual partial-cuts, high-residual partial-cuts, and forested controls). All sites were a minimum of 300 m apart and forested controls were at least 400 m from any logged stands. All logged sites were located adjacent to old (>130 years), aspen-dominated mixed-wood, not to bog, wetland, or conifer-dominated stands.

I changed the initial four treatment types slightly and classified sites as having high, intermediate, or low densities of residual trees based on the number of snags and trees per ha greater than 15 cm in diameter at breast height (DBH), as assessed for a companion study (Chapter 2). The four treatments will henceforth be referred to as "low residual", "intermediate residual", and "high residual" logged sites and forested control. High residual logged sites had 86 to 133 trees per ha, intermediate, 48 to 55 trees per ha, and low, 10 to 36 trees per ha. Forested controls had 246 to 414 trees per ha. Each logged treatment category had four replicates, and there were six forested control sites.

3.2.2 *Artificial Nest Experiment*

I used artificial wicker nests (7 cm in depth and 11 cm in width) with one painted

plasticine and one Chinese painted quail (*Coturnix chinensis*) egg each to obtain an index of relative predation. I did not use Japanese quail (*C. japonica*) eggs because these are larger than most songbird eggs and therefore may not provide accurate measures of small mammal predation (Roper 1992, Haskell 1995a). Chinese painted quail eggs are 19 mm by 25 mm in size, slightly larger than Hermit Thrush (*Catharus guttatus*) eggs (17 mm by 22 mm) (Cotterill 1996). Plasticine eggs were made and painted with two layers of non toxic acrylic paint to resemble quail eggs in size and colour. Plasticine eggs allowed for predator identification while quail eggs provided a reward for predators so they would not learn to avoid artificial nests. To avoid impregnating the nests and eggs with human odour, rubber gloves and boots were worn at all times during handling (Yahner and Voytko 1989, Rudnicky and Hunter 1993). Nests were dipped in mud and lined with dry grasses.

Nests were set out the last week of May, checked every 10 days, and removed after 30 days, approximating the songbird nesting and incubation period in the area. Since nest markers may guide visual predators to nests (Picozzi 1975, Yahner and Wright 1985), I did not mark nests but instead placed a flag 5 to 15 m away from each nest and kept detailed notes on location. All attempts were made to avoid disturbing the surrounding vegetation when checking nests.

I counted a nest as depredated if either one of the two eggs was damaged or missing. I did not include scratches that did not break the shells of quail eggs as evidence of predation because these events would probably not affect chicks inside real eggs. I also did not include marks in plasticine eggs that did not break through the paint because (a) predators that did not break through the paint likely would not break through a shell and (b) these small dents may have occurred while eggs were being transported or placed in nests. I identified predators by examining marks in plasticine eggs. I classified predation events as murid (mouse or vole), avian, or red squirrel. No other predators were identified. Unless the quail egg was obviously pecked, I did not attempt to identify predators if the plasticine egg was missing, instead classifying these as "predator unknown".

3.2.2.1 *Edge Nests*

Thirteen nests were placed in stands adjacent to each logged site and in forested

control sites. Nests were placed within a strip 250 m long and 50 m wide so that all nests were within 50 m of the logged edge. I selected the 50 m width because past research indicates that an edge effect, if present, will be evident within this distance (Paton 1994). Since edge effects have been shown to extend up to 300 m into surrounding stands (Wilcove 1985, Brittingham and Temple 1983, Angelstam 1986), nests were not placed within 300 m of any edge other than that of the treatment stand. A random configuration was produced using a random numbers table (making sure no nests were less than 30 m apart) and nests in all sites were placed according to this configuration. Nine of these nests were placed between 5 cm and 2 m above ground level ("shrub nests"), while the remaining four were placed at the base of trees, logs, or shrubs at ground level ("ground nests"). The proportion of shrub to ground nests was based on the proportion of shrub or tree and ground nesters recorded in the area (Norton and Hannon 1997). I will henceforth refer to stands adjacent to high residual logged sites as "high residual edges", those adjacent to intermediate sites as "intermediate residual edges", and those adjacent to low residual sites as "low residual edges".

3.2.2.2 *Cutblock Nests*

Twenty nests were also placed in residual tree clumps in each intermediate residual, high residual, and forested control site. Nests were not placed in low residual sites because these did not always provide a sufficient number of clumps to allow placement of 20 nests. Nest placement was based on a four by five grid with each nest in a clump of residual trees, 30 to 60 m between nests, and 20 to 240 m between nests and the edge of the logged site. Each nest was placed approximately in the centre of each residual clump so that I could investigate the possible influence of clump size on predation. Fourteen of the nests were placed above ground (5 cm-2 m) and six at ground level.

3.2.3 *Vegetation*

I sampled vegetation in July and August. I measured the distance of each nest from the ground and approximated percentage lateral and overhead cover to assess visibility of each nest. For lateral cover, the observer circled the nest at a distance of 50 cm and approximated the percentage of the nest visible. For overhead cover, the observer estimated the percentage of a 50 cm circle directly above the nest that was covered by

vegetation (Cotterill 1996). One 0.04 ha vegetation plot was centred on each nest to sample vegetation in the area immediately surrounding the nest. I measured canopy cover with a spherical densiometer. I recorded species and classified diameter at breast height (DBH) of all trees (class 1: 8-15 cm; class 2: 15-23 cm; class 3: 23-38 cm; and class 4: >38 cm). I calculated basal area of trees using the median of each DBH class. I estimated ground cover of coarse woody debris, green material (including shrubs, forbs, grasses, sedges, mosses, and ferns), and leaf litter visually in four 1 m^2 plots located at 3 m in each of the four cardinal directions from the centre of the 0.04 ha main plot. I counted shrub stems in five similar 1 m^2 plots at the centre and at 5 m from the centre of each main plot. I also recorded DBH classes of all saplings and poles within a 5 m radius plot centred on the main plot (class 1 = <2.5 cm; class 2 = >2.5 cm, <8 cm). In logged sites, I classified clumps of residual trees (class 1: 1 - 2 trees; class 2: 3 - 10 trees; class 3: >10 trees).

3.2.4 *Analysis*

3.2.4.1 *Nest Predation*

I analyzed predation on artificial nests using generalized linear models with quasi-likelihood functions, scoring depredated nests as 1 and intact nests as 0. The generalized linear model does not assume normally distributed data, while the quasi-likelihood function does not assume any distribution (McCullagh and Nelder 1989). Predicting that nests within each site would not be statistically or biologically independent (Cotterill 1996), I nested site within treatment. I also included measured vegetation variables in the model to investigate the possible effects of these variables on predation. I eliminated variables that did not contribute significantly to the model. This model is the equivalent of a nested logistic regression with none of the standard assumptions about normality or distribution. I used an α-level of 0.10 in all analyses of predation to reduce the probability of committing a Type II error (Schmiegelow et al. 1997). I performed these analyses with the program S-Plus (student version).

3.2.4.2 *Shrub and Ground Nests*

Since I had more shrub than ground nests, I did not compare predation rates on the two types of nests directly but instead used Chi-square contingency tests to investigate whether predation on each nest type was higher than expected. I performed

post-hoc power analyses on these tests using the program G-Power (Faul and Ehrdfelder 1992). I also included nest type and distance of the nest from the ground in all generalized linear models. Distance from the ground was 0 cm for all ground nests.

3.2.4.3 *Plasticine and Quail Eggs*

To investigate whether there was a difference in predation of quail and plasticine eggs, I pooled data from both the edge and the cutblock experiment and compared predation of each egg type among all 474 nests. I performed post-hoc power analyses using the program G-Power (Faul and Ehrdfelder 1992). Since t-tests had low power (<0.65 at $\alpha = 0.10$) (Cohen 1988), I performed a randomized t-test using the program RANDCOMP (Brzustowski 1997). This program calculates the observed mean differences between two groups then randomly selects samples from each group 1000 times and compares the observed mean differences with the distribution of randomly selected mean differences. RANDCOMP provides a p-value that indicates whether or not the observed distribution is significantly different from the randomly selected distribution but it does not provide a test-statistic.

I was unable to test for the preference of specific predators for plasticine or quail eggs because the identity of predators of quail eggs could generally only be inferred from marks left in plasticine eggs, so predators were not identified for predation events in which only the quail egg was depredated. I was able to identify some avian predation events on quail eggs due to the unique tendency of avian predators to peck a hole in the centre of the egg and suck out its contents, however, it is unclear whether avian predation events could be equally well identified for quail and plasticine eggs.

3.2.4.4 *Vegetation*

To investigate changes in vegetation with increasing residual tree density, I compared vegetation variables across treatments. I performed post-hoc power analyses on analyses of variance (ANOVA's) and, finding that most datasets had low power (<0.65 at $\alpha = 0.10$) (Cohen 1988), I performed randomized t-tests as described above. Since RANDCOMP only performs two-way comparisons, I performed multiple t-tests and used a Bonferoni adjustment to correct for multiple comparisons (Zar 1984). I used an α-level of 0.05 in analyses of vegetation.

3.3 Results

3.3.1 *Edge Nests*

A total of 68% of all edge nests were depredated, 82% of all ground nests and 62% of all shrub nests (Table 3.1). Predation was higher on ground than on shrub nests ($\chi^2 = 8.86$, $p = 0.003$). Distance of the nest from the ground (height) was the only variable that significantly predicted probability of predation, with nests closer to the ground more likely to be depredated (Table 3.2). Treatment had no effect on overall predation of edge nests (Figure 3.1). However, residual deviances for all models were not much lower than null deviances, indicating that all of these models were relatively weak and left most of the deviance in predation unexplained (Table 3.2).

I identified predators for 48% of all predation events, 49% of all ground predation events and 47% of all shrub nest predation events (Table 3.1). The most commonly identified predators were murids, with red squirrel and avian predation lower for both nest types (Table 3.1). Treatment was a predictor of red squirrel predation only (Table 3.2), with predation in intermediate residual edges the highest and predation in controls the lowest (Figure 3.1). Nest type and percentage conifer were predictors of murid predation, with higher predation on ground nests and probability of predation decreasing with increasing percentage conifer (Table 3.2). Avian predation decreased with increasing leaf litter (Table 3.2). Neither avian nor murid predation varied significantly with treatment (Figure 3.1). This model was not strong, leaving much of the deviance in total predation unexplained (Table 3.2).

3.3.2 *Cutblock Nests*

A total of 60% of all residual nests were depredated, 77% of all ground nests and 51% of all shrub nests (Table 3.3). Predation was higher on ground than shrub nests ($\chi^2 = 3.05$, $p = 0.081$), and nest type was a significant predictor of predation (Table 3.4). Treatment had no effect on overall predation of nests in logged sites (Table 3.4, Figure 3.2). Again, this model left much of the deviance in total predation unexplained (Table 3.4).

I identified predators for 50% of all predation events, 49% of all ground and 50% of all shrub nest predation events (Table 3.3). The most commonly identified predators were murids, with avian and red squirrel predation lower for total predation and ground

nest predation. Avian predation equaled murid predation of shrub nests (Table 3.3). Neither treatment nor size of residual tree clump was a significant predictor of total predation, nor of predation of any of the identified predators (Table 3.4, Figure 3.2). Nest type was a predictor of total predation and murid predation, with the probability of predation higher for ground than shrub nests (Table 3.4). Avian predation increased with increasing number of shrubs (Table 3.4). Red squirrel predation was not affected by any of the variables measured, including treatment (Table 3.4, Figure 3.2). Again, differences between residual and null deviances were low for all models, indicating that the models were weak and left much of the deviance in predation unexplained (Table 3.4).

3.3.3 *Plasticine and Quail Eggs*

There was no significant difference in total predation of plasticine and quail eggs ($p = 0.244$). A mean of 14.1 (standard error = 1.13) plasticine and 12.2 (standard error = 1.10) quail eggs were depredated per site.

3.3.4 *Vegetation*

Five of the 20 vegetation variables differed significantly among stands adjacent to sites with different densities of residual trees, and 5 more varied between logged sites and forested controls (Table 3.5). Lateral cover of the nest increased with increasing residual tree density and was significantly higher in high residual than low residual edges. Numbers of shrubs and small saplings (< 2.5 cm DBH) were significantly lower in high residual edges than in intermediate or low residual edges. Basal area of deciduous trees was higher in low and intermediate residual edges than in high residual edges, and mean DBH of alder (*Alnus* species) and willow (*Salix* species) (≥ 8 cm DBH) was significantly higher in low than high residual edges. All five of these variables also differed between forested control sites and at least one of the edge sites, as did number and basal area of alder and willow (≥ 8 cm DBH), and number, basal area, and percentage of coniferous trees (Table 3.5).

Five of the 21 vegetation variables differed between high residual and intermediate residual logged sites, while a total of 16 differed between forested controls and at least one of the logged treatments (Table 3.7). Canopy cover and number of deciduous trees were higher in high residual than intermediate residual sites, while conifer basal area, coarse woody debris, and mean DBH of alder and willow (≥ 8 cm

DBH) showed the opposite pattern (Table 3.7). Variables that differed between controls and at least one of the logged treatments were: lateral and overhead cover of the nest, canopy cover, number of shrubs, mean DBH of conifer trees and of alder and willow (≥ 8 cm DBH), number, mean DBH, and basal area of deciduous trees, number of small saplings (<2.5 cm DBH), coarse woody debris, green cover, leaf litter, and number, percentage, and basal area of coniferous trees (Table 3.7).

3.4 Discussion

3.4.1 *Factors Predicting Nest Predation*

The results of this study did not support my predictions that avian, red squirrel, and murid predation would be higher in and adjacent to stands with high vs. low densities of residual trees. I recorded predation events by all three identified predator types in all treatments. Murid predation was higher on nests close to the ground, which is to be expected if red-backed voles accounted for a large proportion of this predation, since these have difficulty climbing (Getz and Ginsberg 1968). Murid predation was also associated with low percentages of conifer. Avian predation was associated with high shrub cover in cutblocks and with low leaf litter in stands adjacent to logged sites. The only predator to show a treatment effect was the red squirrel. As well as being associated with high canopy cover, red squirrel predation was highest in intermediate residual edges, relatively low in low and high residual edges, and very low in forested controls. This pattern did not support the prediction that edge predation would increase with increasing residual tree density.

The pattern in red squirrel predation was largely the effect of an exceptionally high number of red squirrel predation events in one of the four intermediate residual edges. The 50 m by 250 m edge sampled could have been encompassed by one red squirrel territory in these aspen-dominated mixed-wood stands (Rusch and Reeder 1978) and these events may therefore have been the result of one individual red squirrel searching out the artificial nests. Past research on artificial nests in the area does show a clumping of red squirrel predation events (Cotterill 1996). Since the frequency of red squirrel predation was very low, I am not confident that the resulting treatment effect is biologically significant.

None of the models predicting predation were strong, indicating that predation

was not well predicted by the parameters measured either because (a) I did not measure the variables important for predation, or (b) predation is not associated with vegetation or nest site characteristics in the area. Variables that have been found to predict predation in the past include conifer basal area or percentage for red squirrels (King et al. 1998), canopy cover (Hanski et al. 1996), subcanopy height, green cover, and conifer (Song and Hannon in prep.), foliage density and herbaceous cover (Leimgruber et al 1994), nest height (Yahner and Cypher 1987), and nest visibility (Angelstam 1986, Huhta 1995), all of which were tested in this study. Since this is not the only study of nest predation in the boreal mixed-wood that has found little influence of vegetation (Cotterill 1996), I conclude that vegetation is not a good predictor of nest predation in this area. Predation may be incidental, with predators eating eggs when they find them but not foraging for them specifically (Vickery et al. 1992, Howlett and Stutchbury 1996).

3.4.2 *Identified Predators*

The main predators identified in this study were murids. I recorded few avian and red squirrel predation events. The low number of avian predation events may be attributed to low numbers of corvids in the area (S. Hannon unpublished data, S. Song unpublished data). The low number of red squirrel predation events is contrary to the findings of a similar study in the area, which identified red squirrels as the main nest predator in 1993 and 1994 (Cotterill 1996). This difference in red squirrel predation rate may be due to site-specific differences in red squirrel presence or abundance: Cotterill's sites had a higher mean percentage of conifer than my sites, which could translate into higher numbers of red squirrels (King et al. 1998). The difference may also be due to annual differences in the abundance of spruce cones, a preferred food source of red squirrels (Obbard 1987). There was a mast cone crop in 1993 (E. MacDonald pers. comm.) so abundances of red squirrels may have been higher in this and the following year (1994) than in 1997.

In evaluating the effects of different predators, it is important to note that predators were identified for less than half the predation events. I could not identify predators when eggs were missing from the nest. As the smallest potential mammalian predators in the area, murids are the most likely to eat the eggs in or near the nest, as opposed to carrying them away from the nest for consumption. Corvids, red squirrels,

and any other potential mammalian predators may be able to remove the eggs rather than consuming them at the nest. Thus, the fact that I identified more murids than any other predators does not necessarily indicate that these were the most common nest predators, although numbers were high enough to conclude that they were a major cause of nest predation in this study.

3.4.3 *Plasticine and Quail Egg Predation*

Total predation of quail eggs did not differ from total predation of plasticine eggs. It was impossible to compare predation by predator type since predator identification was based primarily on marks in plasticine eggs. Cotterill (1996) and Bayne et al. (1997) suggest that murids may be better able to mark plasticine than quail eggs, however, numerous murid predation events involving both plasticine and quail eggs imply that these predators were able to damage both types of eggs, assuming that whatever depredated the plasticine egg also depredated the quail egg. Since no plasticine egg had marks from more than one type of predator, it is reasonable to assume that most nests were only depredated by one type of predator. Although small mammals could easily be attracted to the odour of plasticine (Cotterill 1996), choice between eggs once they had found the nests would not necessarily be evidence of this attraction.

3.4.4 *Vegetation*

Most of the vegetation variables that differed among forested stands and stands adjacent to sites with varying densities of residual trees could not have varied due to treatment. The only variables that could have varied due to treatment were the number of shrubs and saplings as increased light penetrating into the forest could have facilitated growth. Differences in basal area of deciduous trees, mean DBH, number, and basal area of alder (*Alnus* species) and willow (*Salix* species) (≥ 8 cm DBH), and number, basal area, and percentage of coniferous trees were indicative of a priori differences between sites.

3.4.5 *Comparison with Other Studies in the Area*

Two other nest predation studies performed in the area have also not found higher nest predation in stands adjacent to logged sites (Cotterill 1996, Song and Hannon in prep.). These studies were performed in the first and second year after logging. Although conditions for songbirds in the regenerating stands change rapidly in the first

three years after logging (Chapter 2), results of this study indicate that lack of increased predation is consistent. Lack of increased predation along forest-clearcut edges may be due to the lack of changes in vegetation structure along these ephemeral edges (Ratti and Reese 1988) and to a resulting lack of increases in densities of nesting birds (Song and Hannon in prep), or to the failure of logged sites to serve as predator sources (Andrén 1995).

3.4.6 *Problems with Artificial Nest Experiments*

The use of artificial nests to evaluate nest predation pressure has been heavily criticized (Roper 1992, Leimgruber et al. 1994, Haskell 1995a and 1995b, DeGraaf and Maier 1996, Wilson et al. 1998). Martin (1987) argues that artificial nests overestimate the importance of small mammals as nest predators, since real nests would be guarded by adult birds that would discourage such predators. As olfactory predators, small mammals may also be attracted to the odour of plasticine in artificial nests (Cotterill 1996). In a study by Bayne et al. (1997), predation was higher on ground than shrub nests when plasticine eggs were used but there was no difference between the two nest types when only quail eggs were used. Since murids were responsible for the majority of the ground nest predation events, high predation of plasticine eggs on the ground implies that murids responded to plasticine (Bayne et al. 1997). Regardless of the possible overestimation of mammalian predation, this study demonstrates the same lack of treatment effect if only avian predation is considered.

However, artificial nest experiments may also misrepresent avian predation. Since corvids are visual predators, it has been argued both (a) that avian predation may be underestimated because of the lack of incubating parents providing visual cues (Angelstam 1986) and (b) that avian predation may be overestimated because artificial nests are often more visible than real nests (Angelstam 1986). Whatever the biases, artificial nest experiments do provide a relative index of predation: the biases are the same across treatments (Andrén and Angelstam 1988, Wilson et al. 1998).

3.4.7 *Future Research*

To obtain a real index of nest predation, future studies should involve real rather than artificial nests. Despite the practicality of artificial nest experiments, monitoring real nests in still the only way to discover whether nest predation is really a serious

danger to songbird numbers. For example, the investigation in this study of predation in residual tree clumps in logged sites is based on the assumption that birds are nesting in these clumps. Although it is probable that some birds are nesting in residual tree clumps (Chapter 2), I cannot be sure of this without finding real nests.

Long-term studies should also be carried out to investigate possible changes in songbird and predator community. The area studied is being logged in a two-pass system, whereby approximately half the area of merchantable mixed-wood scheduled for logging is logged at each pass. At the time of this study, only the first pass had been completed, leaving approximately half of the area of merchantable mixed-wood scheduled for logging still untouched. The second pass is scheduled to begin in the year 2004, after which time very few of the aspen-dominated mixed-wood stands in the area will be more than a decade old. Forest birds and predators alike may be forced to make greater use of residual clumps and these could conceivably become 'ecological traps' at this time (Gates and Gysel 1978).

3.4.8 *Conclusions and Management Recommendations*

Leaving high as opposed to low densities of residual trees standing in logged sites in the boreal mixed-wood forest did not result in higher levels of nest predation in residual tree clumps or in stands adjacent to logged sites in the third year after logging. This research supported the findings of other studies in the boreal mixed-wood that did not find increased nest predation in logged sites (Bayne and Hobson 1997) and in forested stands adjacent to logged sites (Cotterill 1996, Bayne and Hobson 1997, Song and Hannon in prep.). Pending further research, from the nest predation perspective there appears to be no immediate harm in nor any benefit to leaving large densities of residual trees in logged stands.

However, from a landscape perspective it may be more harmful to leave high densities of residual trees than to leave low densities or no residual trees in logged sites. Since logging companies remove the same amount of merchantable timber from the landscape whether they are leaving residual trees or not, leaving residual trees would require them to log over a larger area, creating more roads and a broader scale disturbance. The more trees left as residual, the more landscape would have to be disturbed. The benefits of leaving high densities of residual trees should therefore be

careful weighed.

Although the short-term benefits of retaining high densities of residual trees for songbirds in the boreal mixed-wood forest are still questionable (Chapter 2), it is likely that these trees will provide both structural and age diversity and will therefore have a positive effect on regenerating stands (Rose and Muir 1997). For example, residual trees may serve as sources of shelter and seeds for conifer regeneration and sources of snags for birds and mammals, creating stands with more forest species in the future than those created by clearcutting (Rose and Muir 1997).

Since the results of the present study did not indicate that logged sites with residual tree retention were sources of nest predation, I recommend residual trees be retained in logged sites. However, I cannot draw conclusions about how much residual material should be left. The present study and a companion study on songbird abundances (Chapter 2) both indicate that retention of 130 trees/ha does not have largely different effects on songbirds than retention of 10 trees/ha, but both studies were short-term and neither compared the effects of leaving low densities of residual trees to the effects of not leaving any residual trees. Long-term studies are necessary to examine the effects of varying levels of residual tree retention as stands regenerate.

Table 3.1. Predation of shrub and ground nests in stands adjacent to logged sites with low, intermediate, and high densities of residual trees and in forested controls. M = murid predation, R = red squirrel predation, A = avian predation, and Un = unknown predation. The total number of nests in each treatment (N) is presented in parentheses next to the total number of ground, shrub, and all nests depredated.

	Ground Nests					Shrub Nests					All Nests				
Treatment	**M**	**R**	**A**	**Un**	**Total (N)**	**M**	**R**	**A**	**Un**	**Total (N)**	**M**	**R**	**A**	**Un**	**Total (N)**
Low	4	2	3	4	13 (16)	5	3	2	14	24 (36)	9	5	5	18	37 (52)
Intermediate	5	3	0	6	14 (16)	7	6	2	7	22 (36)	12	9	2	13	36 (52)
High	5	1	0	10	16 (16)	4	4	2	16	26 (36)	9	5	2	26	42 (52)
Forested	4	1	1	10	16 (24)	6	1	6	16	29 (54)	10	2	7	26	45 (78)
Total	18	7	4	30	59 (72)	22	14	12	53	101(162)	40	21	16	83	160 (234)

Table 3.2. Results of generalized linear models predicting total, murid, avian, and red squirrel nest predation in stands adjacent to logged sites with low, intermediate, and high densities of residual trees and in forested controls. With predation defined as a categorical variable (1 = depredated, 0 = not depredated), these models are the equivalent of logistic regressions with site nested within treatment.

Dependent Variable	Model	Null Deviance	Residual Deviance	Variables	F-Value	P-Value
Total	2.66 -0.01(Height)	292.03	254.30	Height	8.54	0.004
Murid	-1.06 - 3.75 (% Conifer) - 0.41 (Nest Type)	214.05	198.85	% Conifer	10.08	0.002
				Nest Type	4.76	0.031
Avian	-2.02 - 0.06 (Leaf Litter)	116.73	113.41	Leaf Litter	3.44	0.06
Squirrel	-2.99 - 2.34 (Treatment) + 0.01 (Canopy Cover)	141.31	88.58	Treatment	7.57	0.006
				Canopy Cover	3.11	0.080

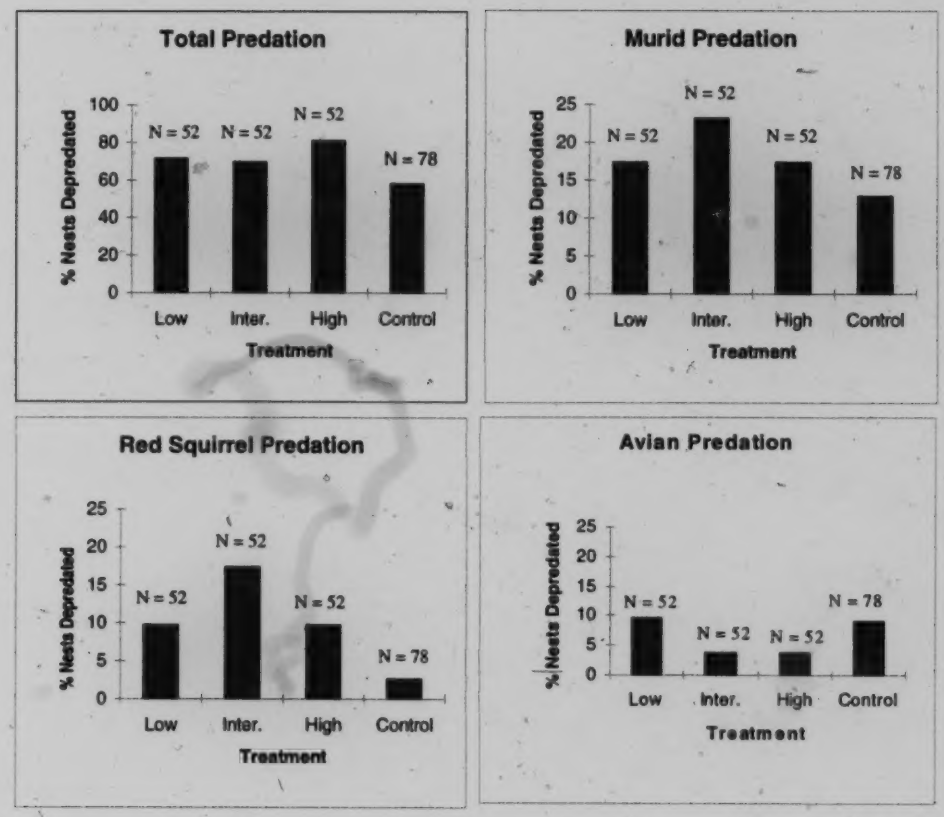

Figure 3.1. Percentage of nests depredated in intermediate (inter.) and high residual logged sites and in forested controls. N = number of nests per treatment.

Table 3.3. Predation of shrub and ground nests in logged sites with intermediate and high densities of residual trees and in forested controls. Nests were placed in residual clumps in logged sites. M = murid predation, R = red squirrel predation, A = avian predation, and Un = unknown predation. The total number of nests in each treatment (N) is presented in parentheses next to the total number of ground, shrub, and all nests depredated.

	Ground Nests					Shrub Nests					All Nests				
Treatment	**M**	**R**	**A**	**Un**	**Total**	**M**	**R**	**A**	**Un**	**Total**	**M**	**R**	**A**	**Un**	**Total**
Intermediate	6	3	2	7	18 (20)	5	2	8	7	22 (37)	11	5	10	14	40 (57)
High	6	1	1	10	18 (22)	2	2	1	10	15 (38)	8	3	2	20	33 (60)
Forest	6	2	5	16	29 (42)	8	5	6	22	41(78)	14	7	11	38	70 (120)
Total	18	6	8	33	65 (84)	15	9	15	39	78 (153)	33	15	23	72	143 (237)

Table 3.4. Results of generalized linear models predicting total, murid, avian, and red squirrel nest predation in logged sites with intermediate and high densities of residual trees and in forested controls. Nests were placed in residual tree clumps in logged sites. With predation defined as a categorical variable (1 = depredated, 0 = not depredated), these models are the equivalent of logistic regressions with site nested within treatment.

Dependent Variable	Model	Null Deviance	Residual Deviance	Variables	F-Value	P-Value
Total	0.63 - 0.60 (Nest Type)	318.35	301.86	Nest Type	16.36	0.00007
Murid	-1.76 - 0.46 (Nest Type)	191.30	185.44	Nest Type	5.82	0.017
Avian	-3.12 + 0.31 (Shrubs)	150.99	145.04	Shrubs	6.24	0.013
Squirrel	No model	-------	-------	-------	-------	-------

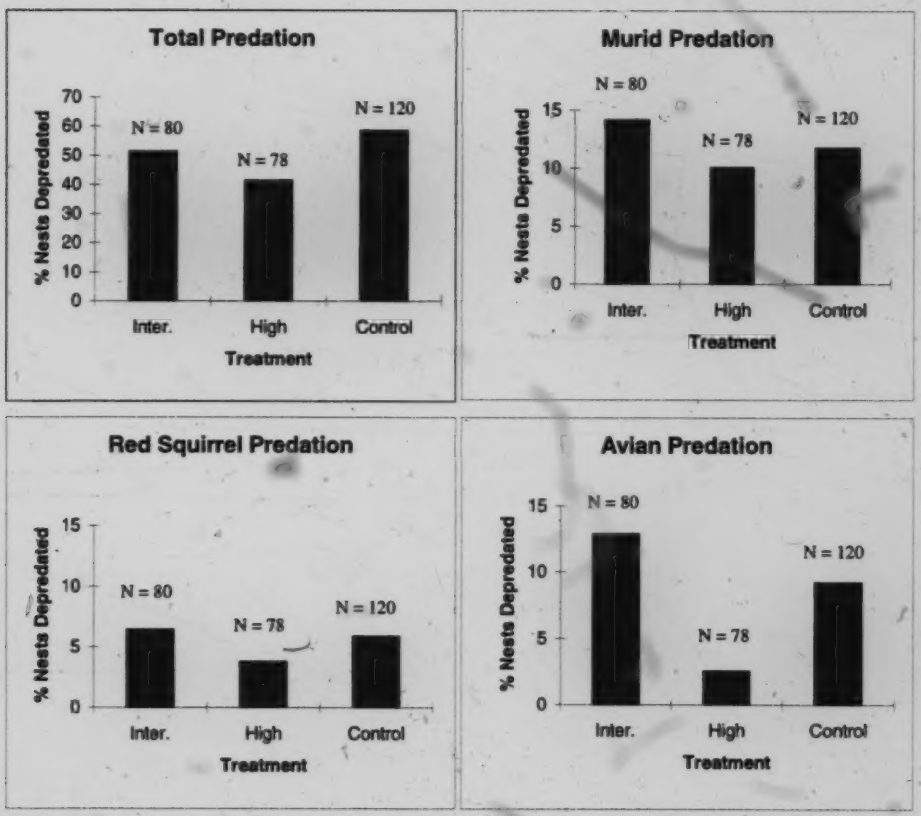

Figure 3.2. Percentage of nests depredated in stands adjacent to low, intermediate (inter.), and high residual logged sites and in forested controls. N = number of nests per treatment.

Table 3.5. Results of randomized t-tests comparing vegetation variables among stands adjacent to logged sites with low, intermediate, and high densities of residual trees and forested control sites. Means are followed by standard errors in parentheses. Variables that differ significantly between treatments are presented in bold. An α level of 0.05 was adjusted for multiple comparisons using a Bonferoni adjustment, so significant differences were judged based on an α-level of 0.008. Letters indicate homogeneous groups. N = 4 for all three logged treatments and N = 6 for controls.

Variable	Low		Intermediate		High		Control	
Height of Nest (cm)	69.3 (7.38)		73.0 (7.31)		64.9 (6.92)		68.8 (5.97)	
Lateral Cover (%)	**26.8 (2.72)**	**a**	**27.5 (2.96)**	**a**	**40.3 (3.87)**	**b**	**25.8 (2.93)**	**a**
Overhead Cover (%)	34.2 (3.81)		38.9 (4.70)		36.6 (4.94)		29.1 (2.97)	
Canopy Cover (%)	80.9 (1.54)		77.7 (1.77)		82.0 (1.80)		78.6 (1.50)	
Debris (%)	10.7 (1.60)		8.7 (0.83)		9.3 (1.28)		8.3 (1.06)	
All Green (%)	76.4 (2.33)		80.5 (1.99)		77.1 (2.09)		81.1 (1.64)	
Leaf Litter (%)	12.0 (1.60)		10.0 (1.01)		12.8 (1.32)		10.3 (1.12)	
Shrubs (#)	**3.6 (0.15)**	**c**	**3.3 (0.17)**	**c**	**1.8 (0.08)**	**a**	**2.5 (0.12)**	**b**
Alder & Willow (#)	**1.3 (0.26)**	**ab**	**1.8 (0.30)**	**b**	**1.5 (0.29)**	**b**	**0.7 (0.16)**	**a**
Alder & Willow DBH (cm)	**16.4 (1.17)**	**c**	**15.0 (0.77)**	**bc**	**13.1 (0.55)**	**ab**	**12.1 (0.42)**	**a**
Alder & Willow BA (cm^2)	**358.2 (90.28)**	**b**	**345.5 (69.01)**	**b**	**244.2 (62.00)**	**b**	**75.1 (16.79)**	**a**
Conifer (#)	**1.9 (0.41)**	**ab**	**1.4 (0.35)**	**a**	**1.4 (0.31)**	**a**	**3.0 (0.47)**	**b**
Conifer DBH (cm)	29.0 (1.96)		25.9 (2.57)		26.4 (2.19)		26.7 (1.20)	
Conifer BA (cm^2)	**1335.0 (294.66)**	**ab**	**710.9 (197.81)**	**a**	**901.2 (222.42)**	**a**	**1597.9 (229.41)**	**b**
Total Deciduous (#)	11.2 (0.86)		11.0 (0.74)		10.6 (0.88)		9.01 (0.53)	
Deciduous DBH (cm)	28.4 (0.67)		28.3 (0.63)		25.7 (0.96)		26.8 (0.82)	
Deciduous BA (cm^2)	**7404.7 (516.53)**	**b**	**7493.6 (458.10)**	**b**	**5699.5 (457.64)**	**a**	**5820.9 (421.47)**	**a**
Percent Conifer (%)	**12.1 (2.45)**	**a**	**10.2 (2.49)**	**a**	**11.3 (2.52)**	**a**	**19.4 (2.47)**	**b**
Small Saplings (#)	**13.4 (1.03)**	**b**	**16.0 (1.14)**	**b**	**7.9 (0.54)**	**a**	**9.4 (0.52)**	**a**
Large Saplings (#)	5.0 (0.47)		5.3 (0.54)		4.0 (0.39)		4.0 (0.33)	

Table 3.6. Results of randomized t-tests comparing vegetation variables among sites with intermediate and high densities of residual trees and forested control sites. Means are followed by standard errors in parentheses. Variables that differ significantly between treatments are presented in bold. An α-level of 0.05 was adjusted for multiple comparisons using a Bonferoni adjustment, so significant differences were judged based on an α-level of 0.017. Letters indicate homogeneous groups. N = 4 for both logged treatments and N = 6 for controls.

Variable	Intermediate		High		Control	
Height of Nest (cm)	66.2 (7.06)		67.6 (7.14)		61.5 (5.15)	
Lateral Cover (%)	**44.7 (3.87)**	**b**	**45.7 (4.11)**	**b**	**26.7 (2.47)**	**a**
Overhead Cover (%)	**49.1 (4.82)**	**b**	**44.9 (4.35)**	**b**	**24.5 (2.78)**	**a**
Canopy Cover (%)	**61.8 (3.64)**	**a**	**77.2 (2.46)**	**b**	**77.4 (1.11)**	**b**
Debris (%)	**11.4 (1.55)**	**b**	**7.3 (1.13)**	**a**	**7.3 (0.65)**	**a**
All Green (%)	**84.6 (1.97)**	**ab**	**88.7 (1.53)**	**b**	**81.7 (1.18)**	**a**
Leaf Litter (%)	**3.9 (0.88)**	**a**	**3.6 (0.75)**	**a**	**10.0 (0.87)**	**b**
Shrubs (#)	**3.0 (0.20)**	**b**	**2.6 (0.28)**	**ab**	**2.3 (0.08)**	**a**
Alder & Willow (#)	1.0 (0.17)		1.0 (0.17)		1.1 (0.16)	
Alder & Willow DBH (cm)	**15.9 (0.77)**	**b**	**12.9 (0.44)**	**a**	**12.5 (0.28)**	**a**
Alder & Willow BA (cm^2)	186.7 (31.93)		147.0 (30.64)		154.8 (31.04)	
Conifer (#)	**1.2 (0.30)**	**a**	**0.2 (0.07)**	**a**	**4.4 (0.57)**	**b**
Conifer DBH (cm)	**17.5 (1.16)**	**a**	**21.2 (3.51)**	**a**	**29.0 (0.90)**	**b**
Conifer BA (cm^2)	**357.2 (104.44)**	**b**	**99.8 (44.00)**	**a**	**2451.4 (263.73)**	**b**
Deciduous (#)	**4.6 (0.48)**	**a**	**7.1 (0.99)**	**b**	**9.7 (0.48)**	**c**
Deciduous DBH (cm)	**24.6 (1.16)**	**a**	**22.8 (1.05)**	**a**	**25.6 (0.48)**	**b**
Deciduous BA (cm^2)	**2413.9 (266.35)**	**a**	**2880.5 (283.51)**	**a**	**5364.2 (268.58)**	**b**
Percent Conifer (%)	**13.1 (3.09)**	**a**	**5.5 (2.42)**	**a**	**23.8 (2.47)**	**b**
Small Saplings (#)	**15.3 (1.71)**	**b**	**14.8 (1.36)**	**b**	**5.8 (0.43)**	**a**
Large Saplings (#)	3.7 (0.49)		2.8 (0.41)		3.2 (0.25)	
Clump Size Class	1.6 (0.13)		1.7 (0.11)		---------	

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CHAPTER 4

THESIS CONCLUSION

4.1 Summary of Results

In this thesis I examined the effects of varying levels of residual tree retention on songbird abundance and community structure in Chapter 2 and on nest predation in Chapter 3. I focused on common forest and open-area species in Chapter 2 and examined differences in songbird abundance and community structure between the first and third year post-logging. I also examined differences between logged sites with varying densities of residual trees and between logged and forested sites. In Chapter 3, I examined predation of artificial nests in forested sites and in and adjacent to logged sites with varying densities of residual trees retained.

4.1.1 *Songbird Abundance and Community Response*

The main results of Chapter 2 were: (a) few species responded to varying densities of residual trees, (b) there were significant differences between logged and forested sites, with more forest birds in forested sites and more open-area birds in logged sites, and (c) there were significant differences in logged sites at a species and a community level between the first and the third year post-logging. Four species increased in abundance with increasing residual tree density in the first year post-logging, while only one increased and one decreased in the third year post-logging. Eleven forest species were recorded at significantly lower abundances in logged than forested sites in the first year and ten in the third year post-logging, but the affected species differed between years: four of the species recorded at lower abundances in logged sites in the first year were not recorded at lower abundances in the third year and three recorded at lower abundances in the third year were not recorded at lower abundances in the first year post-logging. Finally, an influx of open-area species occurred in logged sites between the first and third year post-logging: in the first year, no species were recorded at higher abundance in logged than forested sites but in the third year eight species fit this description, three of which were not recorded in any sites in the first year post-logging. Overall, these open-area species increased in abundance in logged sites with decreasing residual tree density.

4.1.2 *Nest Predation*

Results of Chapter 3 indicated that there were few differences in predation on artificial nests in and adjacent to logged sites with varying densities of residual trees, nor were there differences between these sites and forested control sites. Only predation by red squirrels in stands adjacent to logged sites differed between sites with varying densities of residual trees and forested controls, but this was likely due to clumping of rare red squirrel predation events. I conclude that predation did not increase as a result of logging, regardless of residual tree retention. Other studies of nest predation on artificial nests in the boreal forest have also found no effect of logging on predation, although none of these examined the effect of varying levels of residual tree retention (Cotterill 1996, Bayne and Hobson 1997, Song and Hannon in prep.).

4.2 Recommendations for Future Research

The logged sites studied here were part of the first of a two-pass system of logging, during which approximately half of the area of merchantable aspen-dominated mixed-wood scheduled for logging was removed. The second pass will begin in the area in the year 2004 and will approximately double the area presently disturbed by logging. After the second pass most of the old and mature aspen-dominated mixed-wood stands will have disappeared and the landscape will be dominated by young stands and clearcuts. Although I found little effect of retention of high densities of residual trees in logged sites in the first and third year following the first pass, differences between sites with high and low retention of residual trees may be evident after the second pass.

Residual trees or clumps of trees in logged sites may provide sub-optimal habitat for many forest songbirds. In a landscape that still retains much of its mature and old mixed-wood component, forest species that prefer these habitats may not be forced to settle in the sub-optimal habitat of the residual tree clumps. However, after the second pass, when approximately twice the area that has been logged at present will be logged, optimal habitat will be extremely scarce and songbirds that prefer old or mature forest may have to settle in sub-optimal habitat. At this point it will be important to examine species abundance and nesting success of forest birds in logged sites.

Patterns of nest predation might also change after the second pass. In a landscape with approximately half as many old and mature mixed-wood stand as the present

landscape, predators such as the red squirrel might be stressed for food and have to rely more heavily on eggs. If high densities of birds were nesting in residual tree clumps as a result of a paucity of more suitable habitat, predators might respond by concentrating foraging efforts in these clumps, as suggested by Gates and Gysel (1978). Alternatively, forest predators such as the red squirrel might disappear due to a lack of resources or habitat. If disappearing predators were not replaced by predators better adapted to logged landscapes, such as deer mice (Weaver 1996), nest predation might be lower across the landscape after the second pass.

Regardless of future logging, retention of high densities of residual trees may prove beneficial to songbirds and other wildlife in the future. Residual trees provide structural and age diversity to the regenerating stand, sources of snags, and shelter and seeds to facilitate conifer regeneration (Rose and Muir 1997), all of which may aid in the conservation of forest species in a future logged landscape. Regeneration may not be sufficient after three years to detect these effects.

I therefore recommend that this study be continued, specifically preceding and following logging of the next pass, but also at intervals throughout the next few decades. Changes in songbird abundances and community structure in the first three years following disturbance here and in the first decades elsewhere (Thiollay 1992, Welsh 1992, Pojar 1995, Schieck and Nietfeld 1995) indicate that significant community changes may continue to occur in logged sites regardless of future logging and retention of residual trees may have greater effects on songbird community as the stands regenerate. Furthermore, logging of the second half of the merchantable mixed-wood during the second pass will drastically alter the existing landscape and may therefore cause dramatic changes in songbird community structure and in patterns of nest predation.

I also recommend that a broader range of residual tree retention be examined in future studies. In this study I examined densities of approximately 10 to 133 trees/ha in logged sites. Many logging companies are not leaving densities as high as this. Weyerhaeuser Canada Ltd. (1998) is now leaving 5 to 20 trees/ha, while Alberta Pacific Forest Industries is leaving ~8 trees/ha (Alberta Pacific Forest Industries Inc. 1996). Although I found few differences within the studied range of residual tree retention,

differences might be apparent between sites with retention of 0 and 10 trees/ha. For example, in this study, birds of all nesting and foraging guilds were recorded in logged sites, but logged sites with no residual tree retention would likely provide no habitat for species that depend on trees for nesting or foraging.

We should also examine responses of other taxa to varying densities of residual tree retention. In this study we examined songbirds partly because they are often indicative of general effects of disturbance on the ecosystem (Adams and Barrett 1976, Steele et al. 1984, Croonquist and Brooks 1991), but this is not to imply that other taxa are not important. Research on small mammals, for example, would not only provide insight into the issue of nest predation but would also be useful in itself as an indicator of ecosystem disturbance (Steele et al. 1984, Croonquist and Brooks 1991) and as a step towards conservation of small mammals that might be negatively impacted by logging.

Other taxa that might benefit from residual tree retention include species that make use of the conifer component of the mixed-wood, require uneven-aged stands, and use large trees and snags. Mammalian species that might benefit from retention of residual trees as stands regenerate include forest species such as the marten (*Martes americana*) (Strickland and Douglas 1987) and the fisher (*M. penanti*) (Douglas and Strickland 1987), which favour mixed-age stands and require trees or snags, and the red squirrel, which obtains its main food source from the conifer component of the mixed-wood forest (Obbard 1987). Residual trees may also provide perch sites and nesting trees for raptors. Raptors associated with logged stands with residual tree retention include American Kestrels (*Falco sparverius*) (Nelson and Titus 1989) and Red-tailed Hawks (*Buteo jamaicensis*) (Grimm and Yahner 1985). Residual tree retention might also benefit large cavity nesters such as the Barred Owl (*Strix varia*) by providing large diameter trees and snags for nesting (B. Olsen unpublished data). Raptors that nest in large trees, such as the Bald Eagle (*Haliaeetus leucocephalus*) (Andrew and Mosher 1982), might also benefit.

The potential for residual trees and clumps to serve as stepping stones in dispersal of birds and other taxa must also be investigated. Some forest birds may be unlikely to cross large canopy gaps created by clearcuts (Bierregaard et al. 1992, Desrochers and Hannon 1997). This may limit successful dispersal and eventually result in the isolation

of habitat blocks, which in turn may cause the disappearance of some species from these blocks due to lack of recruitment (Fahrig and Merriam 1994). Research is necessary to evaluate the possible utility of residual trees in mitigating these effects and to investigate whether certain sizes of clumps and distances between clumps have an effect on dispersal.

Finally, we should investigate the potential for logged stands with residual tree retention to buffer the negative effects of wind on forested stands adjacent to logged stands. Conifer trees on the edge of large canopy gaps such as clearcuts may blow over (Navratil et al. 1994). Aspen trees have highly developed root systems and are therefore not likely to blow over but may break due to wind (Peterson and Peterson 1992). If high densities of residual trees reduce the effect of wind on adjacent stands, they might limit the damage caused by the creation of large canopy gaps.

4.3 Implications for Forest Management

Although the focus of this study has been on stand level rather than landscape level effects of residual tree retention, both must be considered in developing recommendations for management. At the stand level, results of this study indicate few differences in songbird community or nest predation between stands of low and high residual tree density. However, there were differences in songbird abundance between logged and forested sites, with forest songbirds being far more abundant in the latter than in the former. Even when high densities of residual trees were retained on logged sites, logging had a deleterious effect on forest songbird abundances. At a landscape level, retention of high rather than low densities of residual trees requires that logging operations be spread out over a larger area to extract the same amount of timber. Based on these considerations, it might be best to leave low (~10 trees/ha) rather than high densities of residual trees (~130 trees/ha), which would allow us to optimize the area of forest left unlogged. However, further research is necessary before conclusions can be drawn and reliable management recommendations formulated.

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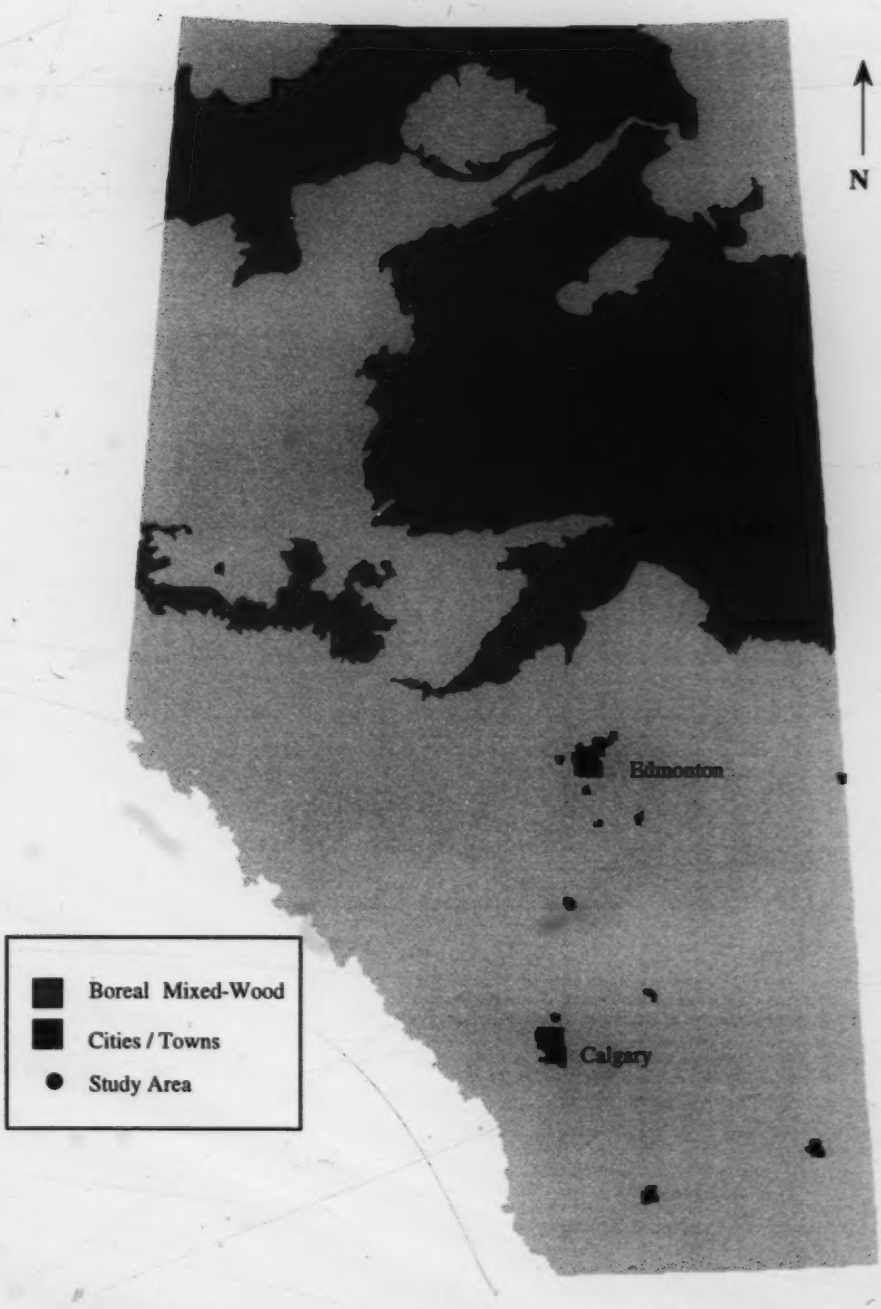


Appendix I. Location of the study site (Calling Lake) within the boreal mixed-wood forest of Alberta.

Appendix II. The study sites north of Calling Lake, Alberta. Numbers represent study sites: 1 = 04841, 2 = 09241, 3 = 10191, 4 = 11141, 5 = 15351, 6 = 15581, 7 = 17391, 8 = 18151, 9 = 18551, 10 = 21431, 11 = 21591, 12 = 22221, 13 = PCC1, 14 = PCC2, 15 = PCC3, 16 = PCC4, 17 = PCC5, 18 = PCC6. "PCC" sites (12 - 18) are forested controls while all others are logged sites. See Appendix 2.5 for details on vegetation.

Appendix 2.1. Mean residual tree density and residual tree retention per hectare for each study site. Residual tree density is the mean number of trees and snags counted per hectare with DBH > 15 cm in 1997. Residual tree retention is a reflection of the percentage of the trees and snags counted in 1994 (before logging) that were also counted in 1997. This measure is calculated by dividing 1997 tree and snag density by 1994 tree and snag density and multiplying by 100. Although all efforts were made to sample the same plots in 1997 as had been sampled in 1994, efforts were not always successful, as evidenced by the 134.9% residual tree retention noted for PCC2. The measure of residual tree retention was used in analyzing turnover in songbird community between pre-logging and post-logging years and residual tree density was used for all other analyses. Missing values represent sites that were not sampled in 1994. Percentages of residual tree retention are also presented for the logged sites studied by Norton and Hannon (1997). Norton and Hannon based their retention percentages on analysis of aerial photographs rather than on ground-level tree counts, but did not quantify retention for forested controls. Missing values therefore correspond to these forested controls and to the six sites not censused in 1994 and 1995 but censused in 1997.

Site	Site #	Treatment	Residual Tree Density (trees/ ha)	Residual Tree Retention (%)	Norton and Hannon (%)
1	10191	Logged	10.4	-------	-------
2	18551	Logged	19.4	-------	-------
3	09241	Logged	28.3	-------	-------
4	15351	Logged	36.1	11.5	7.3
5	17391	Logged	48.3	19.0	6.5
6	18151	Logged	51.7	19.4	31.0
7	11141	Logged	54.2	14.5	28.8
8	22221	Logged	55.6	27.8	23.2
9	21431	Logged	86.1	28.1	6.3
10	15581	Logged	108.3	39.2	21.1
11	04841	Logged	130.6	38.2	36.3
12	21591	Logged	133.3	35.4	38.1
13	PCC3	Forested	246.7	84.6	-------
14	PCC1	Forested	287.5	88.8	-------
15	PCC4	Forested	320.8	-------	-------
16	PCC5	Forested	336.1	-------	-------
17	PCC2	Forested	397.2	134.9	-------
18	PCC6	Forested	414.6	-------	-------

Appendix 2.2. Information on species recorded. Scientific names, foraging guilds, and nesting guilds are noted according to Ehrlich et al. (1988) and migratory strategies, according to Godfrey (1986). Common forest and open-area species are presented in bold. Neotropical migrants (NT) are defined as those wintering south of the United States-Mexico border, short distance migrants (SD) winter in the United States or southern Canada, and residents (R) winter in the boreal forest.

Species	Scientific Name	Code	Migratory Status	Foraging Guild	Nesting Guild
Alder Flycatcher	***Empidonax alnorum***	**ALFL**	**NT**	**Aerial**	**Shrub/Tree**
American Redstart	***Setophaga ruticilla***	**AMRE**	**NT**	**Aerial**	**Shrub/Tree**
American Robin	*Turdus migratorius*	AMRO	SD	Ground	Shrub/Tree
Black-and-white Warbler	*Mniotilta varia*	BAWW	NT	Bark	Ground
Black-throated Green Warbler	***Dendroica virens***	**BGNW**	**NT**	**Foliage**	**Shrub/Tree**
Blackpoll Warbler	*Dendroica striata*	BPWA	NT	Foliage	Shrub/Tree
Brown Creeper	***Certhia americana***	**BRCR**	**R**	**Bark**	**Shrub/Tree**
Canada Warbler	***Wilsonia canadensis***	**CAWA**	**NT**	**Aerial**	**Ground**
Clay-coloured Sparrow	***Spizella pallida***	**CCSP**	**SD**	**Ground**	**Ground**
Chipping Sparrow	***Spizella passerina***	**CHSP**	**NT**	**Ground**	**Shrub/Tree**
Connecticut Warbler	*Oporonis agilis*	COWA	NT	Ground	Ground
Common Yellowthroat	***Geothlypis trichas***	**COYE**	**NT**	**Foliage**	**Shrub/Tree**
Dark-eyed Junco	*Junco hyemalis*	DEJU	SD	Ground	Ground
Hermit Thrush	*Catharus guttatus*	HETH	SD	Ground	Ground
House Wren	*Troglodytes aedon*	HOWR	SD	Ground	Cavity
LeConte's Sparrow	***Ammodramus leconteii***	**LCSP**	**SD**	**Ground**	**Ground**
Least Flycatcher	***Empidonax minimus***	**LEFL**	**NT**	**Aerial**	**Shrub/Tree**
Lincoln's Sparrow	***Melospiza lincolnii***	**LISP**	**NT**	**Ground**	**Ground**
Magnolia Warbler	*Dendroica magnolia*	MAWA	NT	Aerial	Shrub/Tree
Mourning Warbler	***Oporonis philadelphia***	**MOWA**	**NT**	**Foliage**	**Ground**
Ovenbird	***Seiurus auricapillus***	**OVEN**	**NT**	**Ground**	**Ground**
Rose-breasted Grosbeak	***Pheucticus ludovicianus***	**RBGR**	**NT**	**Foliage**	**Shrub/Tree**
Red-breasted Nuthatch	*Sitta canadensis*	RBNU	R	Bark	Cavity
Ruby-crowned Kinglet	*Regulus calendula*	RCKI	SD	Foliage	Shrub/Tree
Red-eyed Vireo	***Vireo olivaceus***	**REVI**	**NT**	**Aerial**	**Shrub/Tree**
Song Sparrow	***Melospiza melodia***	**SOSP**	**SD**	**Ground**	**Ground**
Solitary Vireo	*Vireo solitarius*	SOVI	NT	Foliage	Ground
Sharp-tailed Sparrow	*Ammodramus caudacutus*	STSP	SD	Ground	Ground
Swamp Sparrow	*Melospiza georgiana*	SWSP	NT	Ground	Ground
Swainson's Thrush	***Catharus ustulatus***	**SWTH**	**NT**	**Foliage**	**Shrub/Tree**

Tennessee Warbler	*Vermivora peregrina*	TEWA	NT	Foliage	Ground
Vesper Sparrow	*Pooecetes gramineus*	VESP	NT	Ground	Ground
Warbling Vireo	***Vireo gilvus***	**WAVI**	**NT**	**Foliage**	**Shrub/Tree**
Western Tanager	***Piranga ludoviciana***	**WETA**	**NT**	**Foliage**	**Shrub/Tree**
Winter Wren	***Troglodytes troglodytes***	**WIWR**	**SD**	**Ground**	**Cavity**
White-throated Sparrow	***Zonotrichia albicollis***	**WTSP**	**SD**	**Ground**	**Ground**
Yellow Warbler	***Dendroica petechia***	**YWAR**	**NT**	**Foliage**	**Shrub/Tree**
Yellow-rumped Warbler	***Dendroica coronata***	**YRWA**	**SD**	**Foliage**	**Shrub/Tree**

Appendix 2.3. Total number of birds recorded in logged and forested sites in the year before (1994) and in two years after logging (1995 and 1997). Singing males were assigned a score of 1, calling or silent individuals a score of 0.5. Twelve forested sites were censused in 1994, 3 forested sites and 9 logged sites were censused in 1995, and 6 forested and 12 logged sites were censused in 1997. Common forest (abundant before logging) and open-area (more abundant in logged than forested sites after logging) species are presented in bold, while all other species were recorded at low abundances before and after logging.

Species	1994	1995			1997		
	Total	Control	Logged	Total	Control	Logged	Total
Alder Flycatcher	**0**	**0**	**4.0**	**4.0**	**0**	**28.0**	**28.0**
American Redstart	**45.0**	**15.0**	**6.5**	**21.5**	**19.0**	**3.0**	**21.0**
American Robin	4.0	0	6.5	6.5	6.0	13.0	19.0
Black-and-white Warbler	0	3.0	1.5	4.5	2.0	2.0	4.0
Black-throated Green Warbler	**44.0**	**12.0**	**3.0**	**15.0**	**24.0**	**3.0**	**27.0**
Blackpoll Warbler	0	0	0	0	2.0	0	2.0
Brown Creeper	**17.0**	**3.0**	**3.0**	**6.0**	**1.5**	**0**	**15.0**
Canada Warbler	**18.0**	**3.0**	**0**	**3.0**	**3.0**	**0**	**3.0**
Clay-coloured Sparrow	**0**	**0**	**2.0**	**2.0**	**0**	**23.5**	**23.5**
Chipping Sparrow	**14.0**	**7.0**	**41.0**	**48.0**	**12.0**	**17.0**	**29.0**
Connecticut Warbler	0	0	0	0	7.0	25.0	32.0
Common Yellowthroat	**0**	**0**	**0**	**0**	**0**	**29.0**	**29.0**
Dark-eyed Junco	0	2.0	4.0	6.0	3.0	6.0	9.0
Hermit Thrush	0	3.0	2.5	5.5	0	0	0
House Wren	0	3.0	3.0	6.0	8.0	9.5	17.5
LeConte's Sparrow	**0**	**0**	**0**	**0**	**2.0**	**37.0**	**39.0**
Least Flycatcher	**19.0**	**6.0**	**6.0**	**12.0**	**8.0**	**20.5**	**28.5**
Lincoln's Sparrow	**6.0**	**3.0**	**19.0**	**22.0**	**0**	**55.5**	**55.5**
Magnolia Warbler	3.0	0	0	0	0	0	0
Mourning Warbler	**70.0**	**22.0**	**27.0**	**49.0**	**21.0**	**79.0**	**100.0**
Ovenbird	**13.0**	**13.0**	**5.0**	**18.0**	**15.0**	**3.0**	**18.0**
Rose-Breasted Grosbeak	**11.5**	**9.0**	**4.0**	**13.0**	**18.0**	**29.0**	**47.0**
Red-breasted Nuthatch	6.5	0.5	0	0.5	2.0	6.0	8.0
Ruby-crowned Kinglet	3.0	3.0	0	3.0	2.0	2.0	4.0
Red-eyed Vireo	**59.0**	**19.0**	**17.0**	**36.0**	**21.0**	**18.0**	**39.0**
Song Sparrow	**0**	**0**	**0**	**0**	**0**	**8.0**	**8.0**
Solitary Vireo	3.0	0	3.0	3.0	2.0	2.0	4.0
Sharp-tailed Sparrow	0	0	0	0	0	2.0	2.0
Swamp Sparrow	0	0	0	0	2.0	9.0	11.0
Swainson's Thrush	**31.5**	**9.5**	**4.5**	**14.0**	**10.5**	**3.0**	**13.5**

Tennessee Warbler	8.0	18.0	21.0	39.0	64.0	109.5	173.5	
Vesper Sparrow	0	0	0	0	0	3.0	3.0	
Warbling Vireo	**13.0**	**4.0**	**6.0**	**10.0**	**2.0**	**0**	**2.0**	
Western Tanager	**17.0**	**3.0**	**2.0**	**5.0**	**7.0**	**0**	**7.0**	
Winter Wren	**14.0**	**7.0**	**8.0**	**15.0**	**10.0**	**4.5**	**14.5**	
White-throated Sparrow	**106.5**	**27.5**	**80.0**	**107.5**	**33.5**	**92.5**	**126.0**	
Yellow Warbler	**13.0**	**9.0**	**5.0**	**14.0**	**10.5**	**18.5**	**29.0**	
Yellow-rumped Warbler	**42.0**	**22.0**	**23.5**	**45.5**	**12.0**	**14.0**	**26.0**	

Appendix 2.4. Mean abundances per station in logged and forested sites in the year before (1994) and in two years after the logging (1995 and 1997). Singing males were assigned a score of 1, calling or silent individuals a score of 0.5. Twelve forested sites were censused in 1994, 3 forested sites and 9 logged sites were censused in 1995, and 6 forested and 12 logged sites were censused in 1997. Common forest (abundant before logging) and open-area (more abundant in logged than forested sites after logging) species are presented in bold, while all other species were recorded at low abundances before and after logging. Standard errors follow means in parentheses.

Species	1994	1995			1997		
	Total	Control	Logged	Total	Control	Logged	Total
Alder Flycatcher	**0.12 (0.09)**	**0**	**0.16 (0.11)**	**0.12 (0.09)**	**0**	**0.47 (0.12)**	**0.31 (0.09)**
American Redstart	**0.38 (0.16)**	**1.14 (0.33)**	**0.16 (0.09)**	**0.40 (0.16)**	**0.74 (0.26)**	**0.05 (0.05)**	**0.28 (0.12)**
American Robin	0.13 (0.05)	0	0.17 (006)	0.13 (0.05)	0.32 (0.15)	0.23 (0.07)	0.26 (0.12)
Black-and-white Warbler	0.06 (0.06)	0.29 (0.20)	0.03 (0.02)	0.10 (0.06)	0.07 (0.05)	0.03 (0.02)	0.05 (0.02)
Black-throated Green Warbler	**0.23 (0.11)**	**0.87 (0.13)**	**0.07 (0.03)**	**0.27 (0.11)**	**0.95 (0.31)**	**0.05 (0.03)**	**0.35 (0.14)**
Blackpoll Warbler	0	0	0	0	0.07 (0.05)	0	0.02 (0.02)
Brown Creeper	**0.07 (0.06)**	**0.28 (0.20)**	**0.07 (0.06)**	**0.13 (0.07)**	**0.05 (0.03)**	**0**	**0.02 (0.01)**
Canada Warbler	**0.05 (0.03)**	**0.19 (0.12)**	**0**	**0.05 (0.03)**	**0.10 (0.10)**	**0**	**0.03 (0.03)**
Clay-coloured Sparrow	**0**	**0**	**0.06 (0.04)**	**0.04 (0.03)**	**0**	**0.41 (0.13)**	**0.27 (0.10)**
Chipping Sparrow	**0.57 (0.11)**	**0.48 (0.08)**	**1.01 (0.17)**	**0.88 (0.14)**	**0.47 (0.10)**	**0.34 (0.06)**	**0.38 (0.05)**
Connecticut Warbler	0	0	0	0	0.33 (0.16)	0.40 (0.12)	0.38 (0.09)
Common Yellowthroat	**0**	**0**	**0**	**0**	**0**	**0.51 (0.13)**	**0.34 (0.10)**
Dark-eyed Junco	0.04 (0.03)	0.17 (0.10)	0.09 (0.04)	0.11 (0.04)	0.15 (0.08)	0.10 (0.03)	0.12 (0.03)
Hermit Thrush	0.10 (0.06)	0.28 (0.20)	0.05 (0.02)	0.11 (0.06)	0	0	0
House Wren	0.04 (0.03)	0	0.06 (0.04)	0.04 (0.03)	0.27 (0.10)	0.16 (0.05)	0.20 (0.05)
LeConte's Sparrow	**0**	**0**	**0**	**0**	**0.06 (0.04)**	**0.66 (0.13)**	**0.46 (0.11)**
Least Flycatcher	**0.23 (0.09)**	**0.47 (0.10)**	**0.20 (0.11)**	**0.27 (0.09)**	**0.24 (0.14)**	**0.44 (0.10)**	**0.38 (0.08)**
Lincoln's Sparrow	**0.36 (0.14)**	**0.23 (0.05)**	**0.44 (0.13)**	**0.39 (0.10)**	**0**	**1.01 (0.11)**	**0.67 0.14)**
Magnolia Warbler	0.02 (0.02)	0	0	0	0	0	0
Mourning Warbler	**0.96 (0.18)**	**1.51 (0.36)**	**0.77 (0.17)**	**0.96 (0.18)**	**0.86 (0.12)**	**1.52 (0.14)**	**1.30 (0.13)**
Ovenbird	**0.09 (0.05)**	**0.35 (0.02)**	**0**	**0.09 (0.05)**	**0.55 (0.17)**	**0.10 (0.08)**	**0.25 (0.09)**
Rose-Breasted Grosbeak	**0.13 (0.06)**	**0.75 (0.30)**	**0.09 (0.04)**	**0.25 (0.11)**	**0.75 (010)**	**0.46 (0.10)**	**0.56 (0.08)**
Red-breasted Nuthatch	0.01 (0.01)	0.06 (0.06)	0	0.01 (0.01)	0.07 (0.05)	0.14 (0.05)	0.12 (0.04)
Ruby-crowned Kinglet	0.04 (0.03)	0.28 (0.20)	0	0.07 (0.06)	0.06 (0.06)	0.04 (0.03)	0.04 (0.02)
Red-eyed Vireo	**0.66 (0.19)**	**1.39 (0.34)**	**0.41 (0.17)**	**0.66 (0.19)**	**0.83 (0.09)**	**0.36 (0.11)**	**0.51 (0.10)**
Song Sparrow	**0**	**0**	**0.08 (0.08)**	**0**	**0**	**0.12 (0.05)**	**0.08 (0.03)**
Solitary Vireo	0	0	0	0	0.06 (0.04)	0.03 (0.03)	0.04 (0.03)
Sharp-tailed Sparrow	0	0	0	0	0	0.06 (0.06)	0.04 (0.04)
Swamp Sparrow	0	0	0	0	0.06 (0.04)	0.17 (0.05)	0.13 (0.04)

Swainson's Thrush	**0.26 (0.11)**	**0.67 (0.17)**	**0.16 (0.11)**	**0.29 (0.11)**	**0.34 (0.14)**	**0.04 (0.04)**	**0.14 (0.06)**
Tennessee Warbler	0.66 (0.14)	1.24 (0.12)	0.55 (0.11)	0.73 (0.12)	2.41 (0.41)	2.09 (0.22)	2.20 (0.19)
Vesper Sparrow	0	0	0	0	0	0.04 (0.03)	0.03 (0.02)
Warbling Vireo	**0.15 (0.09)**	**0.23 (0.15)**	**0.20 (0.12)**	**0.21 (0.09)**	**0.09 (0.06)**	**0**	**0.03 (0.02)**
Western Tanager	**0.03 (0.03)**	**0.18 (0.10)**	**0.11 (0.11)**	**0.13 (0.09)**	**0.30 (0.12)**	**0**	**0.10 (0.05)**
Winter Wren	**0.23 (0.08)**	**0.52 (0.08)**	**0.20 (0.09)**	**0.28 (0.08)**	**0.40 (0.17)**	**0.10 (0.05)**	**0.20 (0.07)**
White-throated Sparrow	**1.29 (0.13)**	**1.87 (0.27)**	**1.99 (0.29)**	**1.96 (0.22)**	**1.11 (0.30)**	**1.75 (0.12)**	**1.53 (0.14)**
Yellow Warbler	**0.22 (0.08)**	**0.62 (0.29)**	**0.18 (0.07)**	**0.29 (0.10)**	**0.42 (0.10)**	**0.34 (0.08)**	**0.36 (0.06)**
Yellow-rumped Warbler	**0.37 (0.13)**	**1.58 (0.09)**	**0.67 (0.17)**	**0.90 (0.07)**	**0.50 (0.08)**	**0.33 (0.09)**	**0.38 (0.07)**

Appendix 2.5. Vegetation variables measured in three 0.04 ha plots 30 m from each sample station at 0°, 120°, and 240° in 1997. Residual is the mean per hectare and all other variables, means per plot. Logged sites are denoted by numbers (e.g., 04841) and forested controls by the prefix PCC (e.g., PCC1).

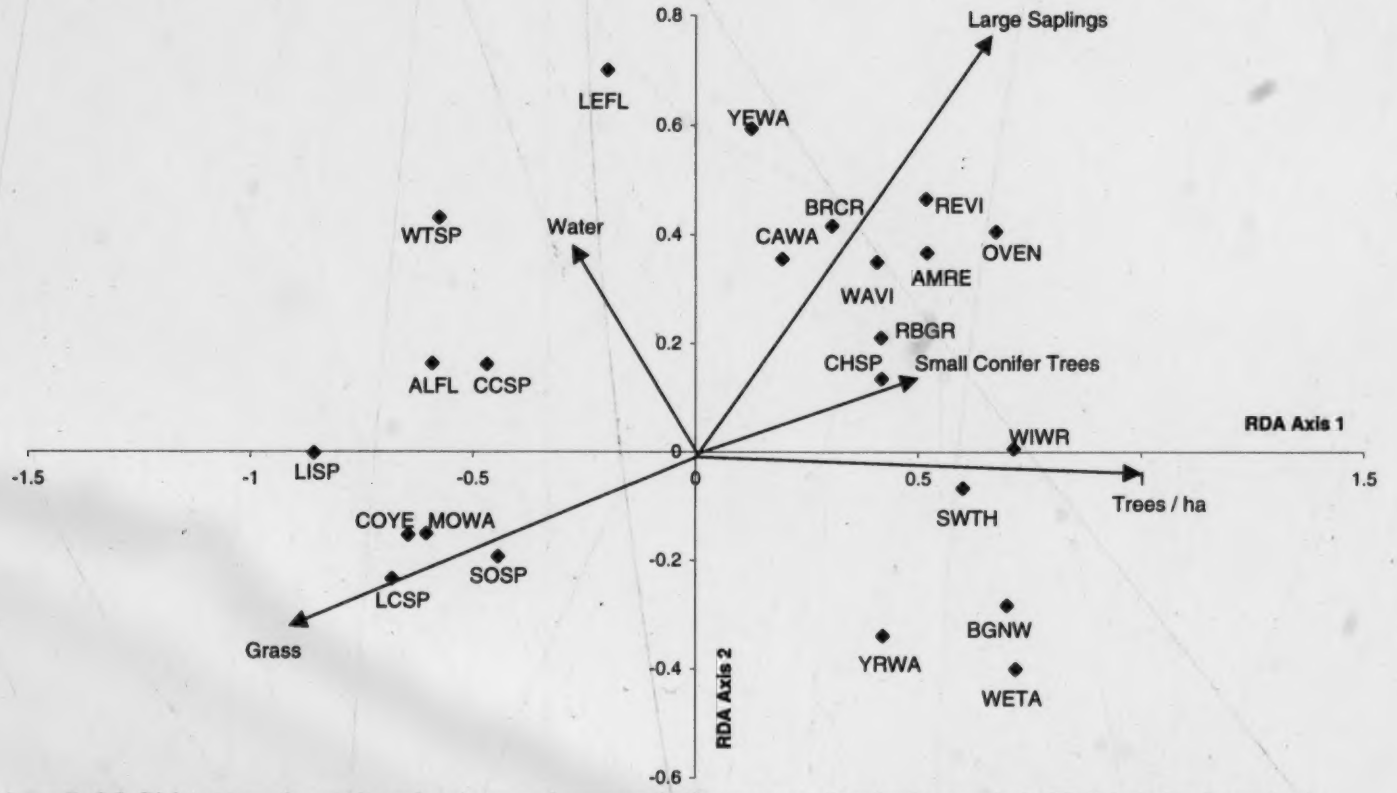
site	04841	09241	10191	11141	15351	15581
Plots (#)	18	15	12	12	18	6
Residual Trees / ha (#)	130.6	28.3	10.4	54.2	36.1	108.3
Canopy Cover (%)	41.0	2.0	0	15.0	2.0	42.0
Canopy Height (m)	24.9	18.0	26.3	24.9	25.4	22.6
Subcanopy Height (m)	10.8	6.0	6.5	16.0	12.0	23.7
Tall Shrub Height (m)	3.2	1.5	2.0	2.5	2.5	2.9
Alder & Willow Class 1 (#)	0.1	0.1	0.1	0.2	0.1	1.0
Alder & Willow Class 2 (#)	0.2	0	0	0	0	0
Alder & Willow Class 3 (#)	0	0	0	0	0	0
Alder & Willow Class 4 (#)	0	0	0	0	0	0
Total Alder & Willow (#)	0.2	0.1	0.1	0.2	0.1	1.0
Alder & Willow DBH (cm)	17.13	11.50	11.50	11.50	11.50	11.50
Alder & Willow BA (cm^2)	53.00	6.92	8.65	17.30	11.54	103.82
Conifer Class 1 (#)	0.1	0.3	0	0	0.1	0
Conifer Class 2 (#)	0.1	0	0	0	0.1	0
Conifer Class 3 (#)	0.2	0.4	0.1	0	0.1	0
Conifer Class 4 (#)	0	0.1	0	0	0	0
Total Conifer (#)	0.4	0.7	0.2	0	0.2	0
Conifer DBH (cm)	24.5	26.47	30.50	0	18.13	0
Conifer BA (cm^2)	205.30	412.1	60.85	0	67.85	0
Deciduous Class 1 (#)	1.2	0.3	0	0.7	1.0	5.2
Deciduous Class 2 (#)	1.6	0.3	0.2	0.2	0.3	2.2
Deciduous Class 3 (#)	1.2	0.1	0.1	0.7	0.1	0.3
Deciduous Class 4 (#)	0.8	0	0	0.7	0.4	1.0
Total Deciduous (#)	4.8	0.7	0.3	2.3	1.9	8.7
Deciduous DBH (cm)	26.49	17.70	21.88	29.68	25.82	20.85
Deciduous BA (cm^2)	2547.23	177.75	131.70	1558.7	894.86	2778.54
Percent Conifer (%)	10.7	48.1	25.0	0	17.9	0
Snags (#)	1.1	0.3	0	0.6	0.4	0.8
Snag Bark (%)	46.8	13.3	0	45.4	26.0	35.4
Snag Height (m)	7.8	8.1	0	12.2	5.7	4.5
Snag DBH (cm)	22.15	3.07	0	17.33	8.58	26.42
Snag BA (cm^2)	1415.37	147.16	0	562.71	377.04	1016.90
Leaf Litter Depth (cm)	9.92	10.33	9.98	9.83	8.71	12.88
Shrubs (#)	6.2	1.4	2.3	3.2	3.2	4.4
Shrub Species (#)	5.7	2.3	4.1	4.8	5.4	5.3
Large Saplings (#)	3.5	0.2	0.6	1.2	1.1	7.0
Small Saplings (#)	22.1	7.6	12.3	26.1	22.2	22.5
Green Cover (%)	79.7	71.4	87.2	90.9	89.1	88.5
Grass Cover (%)	30.7	36.0	49.8	50.8	44.8	8.1
Shrub Cover (%)	27.1	12.6	18.8	27.5	26.8	53.3
Forb Cover (%)	20.3	19.5	13.4	11.9	14.7	24.6
Moss & Fern Cover (%)	1.6	3.3	5.1	0.7	2.7	2.5
Coarse Woody Debris Cover (%)	11.5	20.0	6.5	6.0	7.7	7.5
Leaf Litter Cover (%)	8.8	3.8	2.4	3.0	3.2	4.0

Appendix 2.5 continued

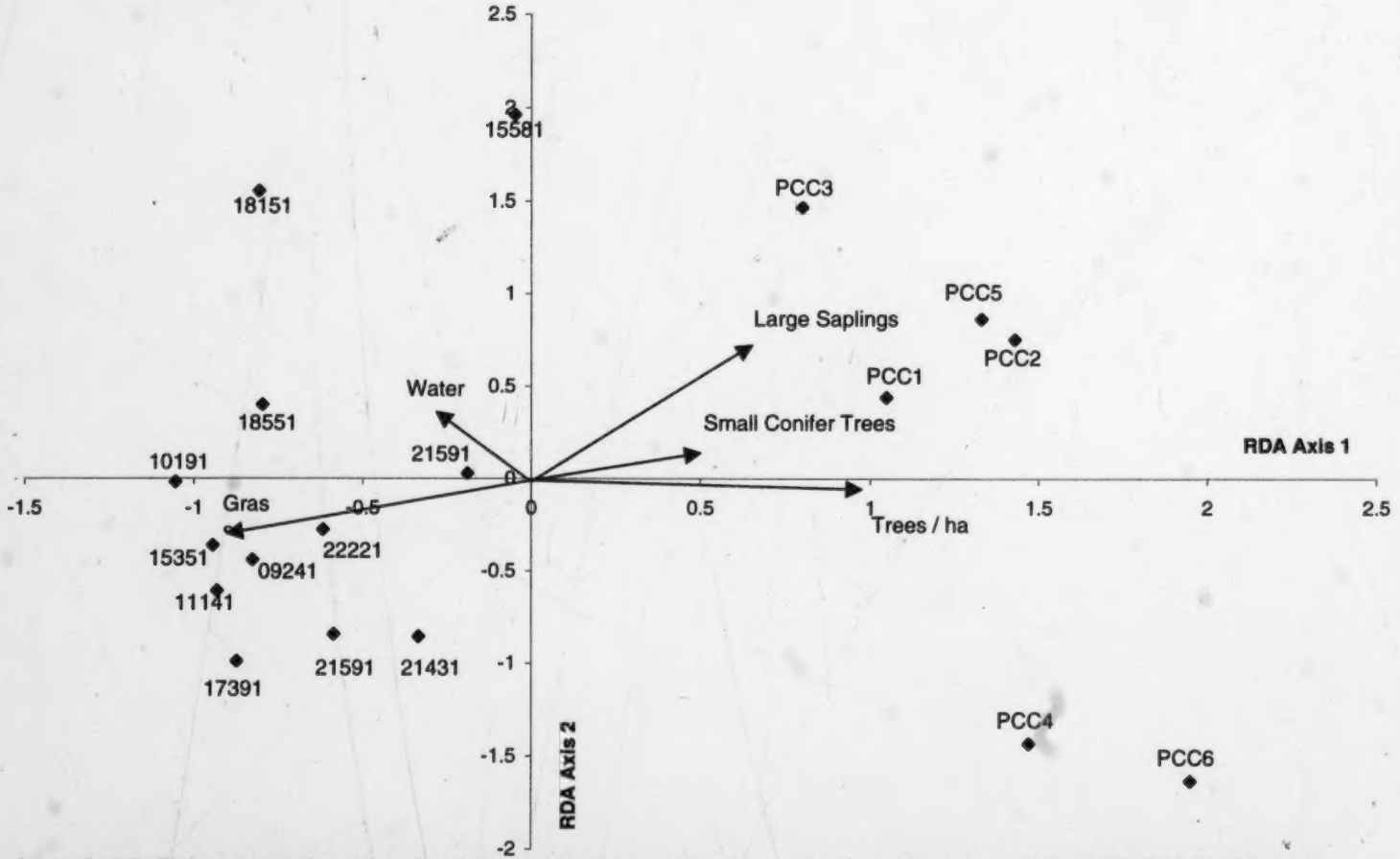
site	17391	18151	18551	21431	21591	22221
Plots (#)	15	15	18	9	6	18
Residual Trees / ha (#)	48.3	51.7	19.4	86.1	133.3	55.6
Canopy Cover (%)	5.0	31.0	7.0	13.0	33.0	10.0
Canopy Height (m)	22.7	26.0	23.2	22.0	23.9	24.3
Subcanopy Height (m)	13.0	9.2	0	0	15.6	12.8
Tall Shrub Height (m)	2.1	2.5	2.0	2.2	2.2	1.9
Alder & Willow Class 1 (#)	0	0.5	0.1	0	0.5	0.6
Alder & Willow Class 2 (#)	0	0.1	0	0.2	0.3	0
Alder & Willow Class 3 (#)	0	0	0	0	0	0
Alder & Willow Class 4 (#)	0	0	0	0	0	0
Total Alder & Willow (#)	0	0.7	0.1	0.2	0.8	0.6
Alder & Willow DBH (cm)	0	13.38	11.50	19.00	13.38	11.50
Alder & Willow BA (cm^2)	0	93.15	5.77	62.97	146.37	63.44
Conifer Class 1 (#)	0	0.4	0	0	0	0
Conifer Class 2 (#)	0.1	0.1	0	0.2	0.2	0
Conifer Class 3 (#)	0.2	0.1	0	0.6	0	0.1
Conifer Class 4 (#)	0	0.1	0	0	0	0.1
Total Conifer (#)	0.3	0.7	0	0.8	0.2	0.1
Conifer DBH (cm)	25.90	16.75	0	24.75	19.00	36.25
Conifer BA (cm^2)	183.83	220.31	0	468.67	47.23	117.50
Deciduous Class 1 (#)	0	1.2	0.3	0	3.2	0.7
Deciduous Class 2 (#)	0.7	0.5	0.2	0.6	1.00	0.3
Deciduous Class 3 (#)	0.1	0.5	0.2	1.1	1.7	0.6
Deciduous Class 4 (#)	0	0.1	0.1	0	1.2	0.3
Total Deciduous (#)	0.7	2.3	0.8	1.7	7.0	1.9
Deciduous DBH (cm)	20.92	20.65	26.38	27.82	24.04	28.44
Deciduous BA (cm^2)	237.61	782.24	392.21	968.82	3444.74	1036.71
Percent Conifer (%)	23.8	19.1	0	20.8	2.0	7.8
Snags (#)	0.9	0.6	0.3	0.8	1.0	0.9
Snag Bark (%)	15.2	30.2	17.9	25.8	49.4	41.2
Snag Height (m)	1.1	7.2	11.2	11.0	12.6	13.1
Snag DBH (cm)	1.91	11.70	7.64	15.78	15.17	15.65
Snag BA (cm^2)	392.02	497.21	267.53	665.85	622.11	688.65
Leaf Litter Depth (cm)	3.97	8.83	7.43	14.03	7.29	10.68
Shrubs (#)	2.6	2.6	2.4	2.2	2.4	1.8
Shrub Species (#)	4.2	5.0	4.1	3.7	4.3	3.4
Large Saplings (#)	0	4.5	1.1	1.0	2.0	0.9
Small Saplings (#)	9.9	13.7	14.3	24.6	16.7	8.1
Green Cover (%)	83.5	86.7	76.5	87.8	86.2	75.4
Grass Cover (%)	47.9	43.3	38.5	43.3	43.5	37.1
Shrub Cover (%)	11.5	21.2	16.9	19.0	20.4	14.9
Forb Cover (%)	20.3	18.2	19.3	22.9	20.0	16.9
Moss & Fern Cover (%)	3.7	4.0	1.7	2.5	2.3	6.5
Coarse Woody Debris Cover (%)	10.7	7.0	16.5	10.7	7.9	20.6
Leaf Litter Cover (%)	1.1	0.8	1.5	1.5	5.8	1.4

Appendix 2.5 continued

site	PCC1	PCC2	PCC3	PCC4	PCC5	PCC6
Plots (#)	18	9	15	6	18	12
Residual Trees / ha (#)	287.5	397.2	246.7	320.8	336.1	414.6
Canopy Cover (%)	68.0	61.0	82.0	77.0	71.0	75.0
Canopy Height (m)	29.2	22.2	27.3	29.6	27.8	28.3
Subcanopy Height (m)	12.6	10.0	0	14.2	12.5	15.7
Tall Shrub Height (m)	4.5	4.1	3.2	4.6	4.0	6.0
Alder & Willow Class 1 (#)	1.7	1.3	1.6	0.3	0.3	0.4
Alder & Willow Class 2 (#)	0.3	0.6	0.5	0	0.1	0.2
Alder & Willow Class 3 (#)	0	0	0.4	0	0	0.1
Alder & Willow Class 4 (#)	0	0	0	0	0.1	0
Total Alder & Willow (#)	1.9	1.9	2.5	0.3	0.4	0.7
Alder & Willow DBH (cm)	12.58	12.63	15.30	11.50	16.05	15.47
Alder & Willow BA (cm^2)	251.75	295.86	609.34	34.61	127.28	174.96
Conifer Class 1 (#)	0.4	6.4	0.1	0.3	0.7	1.5
Conifer Class 2 (#)	0.9	2.8	0	0	0.4	1.7
Conifer Class 3 (#)	0.8	0.9	0	0.5	0.8	1.8
Conifer Class 4 (#)	0.6	0.4	0	1.7	0.5	1.9
Total Conifer (#)	2.7	10.5	0.1	2.5	2.4	6.9
Conifer DBH (cm)	28.08	26.91	11.50	33.14	31.80	28.90
Conifer BA (cm^2)	1722.21	2720.77	6.92	2707.63	1461.27	4620.90
Deciduous Class 1 (#)	1.6	1.0	1.1	1.3	2.6	0.9
Deciduous Class 2 (#)	1.6	2.0	1.2	0.5	2.4	0.7
Deciduous Class 3 (#)	2.1	3.1	2.6	3.8	4.1	5.4
Deciduous Class 4 (#)	2.0	3.8	3.7	3.7	2.6	1.2
Total Deciduous (#)	7.3	9.9	8.6	9.3	11.6	8.3
Deciduous DBH (cm)	26.34	30.33	31.55	31.87	27.50	28.42
Deciduous BA (cm^2)	4894.37	8173.7	7433.74	8156.77	7442.62	5994.13
Percent Conifer (%)	17.8	13.2	0.3	18.9	14.6	41.8
Snags (#)	3.3	2.3	1.5	2.7	2.6	3.4
Snag Bark (%)	78.1	77.2	56.4	69.4	79.0	80.7
Snag Height (m)	8.0	10.3	8.1	6.4	8.0	14.4
Snag DBH (cm)	32.27	28.14	24.80	27.30	30.89	24.71
Snag BA (cm^2)	2721.18	1903.72	1506.96	2295.44	1943.73	1719.03
Leaf Litter Depth (cm)	10.36	9.72	12.68	10.50	11.11	10.92
Shrubs (#)	4.2	4.7	5.2	4.1	4.6	2.7
Shrub Species (#)	5.7	4.7	5.6	6.0	5.9	3.7
Large Saplings (#)	6.2	5.8	8.7	2.7	8.7	3.5
Small Saplings (#)	7.3	5.9	12.0	17.0	12.8	7.2
Snag Height (m)	8.5	12.1	12.8	7.7	8.8	15.4
Green Cover (%)	80.0	78.7	82.9	78.5	76.8	71.0
Grass Cover (%)	16.5	3.6	6.6	6.0	6.0	6.0
Shrub Cover (%)	25.3	24.4	41.1	37.5	32.5	17.3
Forb Cover (%)	30.9	39.2	31.2	31.2	35.5	37.9
Moss & Fern Cover (%)	7.2	11.5	4.1	3.7	2.8	9.8
Coarse Woody Debris Cover (%)	8.3	8.6	7.7	10.0	7.8	8.2
Leaf Litter Cover (%)	7.5	8.7	9.3	11.5	15.3	20.7



Appendix 2.6. Biplot representing species and environmental scores on the first two axes of a redundancy analysis (RDA) including forested and logged sites and all common forest and open-area birds. Eigenvalues are 0.373 and 0.103 for the first and second axes respectively. The first axis explains 37.7% of the variation in species data and the second, 10.2%. See Appendix 2.2 for full species names.



Appendix 2.7. Biplot representing site and environmental scores on the first two axes of a redundancy analysis (RDA) including forested (PCC1 to PCC6) and logged sites (all numbered sites without the prefix PCC) and all common forest and open-area birds. Eigenvalues are 0.373 and 0.103 for the first and second axes respectively. The first axis explains 37.7% of the variation in species data and the second, 10.2%. See Appendix 2.5 for details on site vegetation.